University of Alberta

Use of remotely sensed data to assess Neotropical dry forest structure and diversity

by

Margaret Erika Rose Kalacska ©

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the requirements for the degree of *Doctor of Philosophy*

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DEDICATION

For Szuli (Tapsi)

ABSTRACT

Due to a number of socioeconomic and environmental factors the tropical dry forest has been among the most anthropogenically disturbed, least protected and understudied systems. By taking advantage of the available satellite imagery and investigating the possibility of using these data for inferring characteristics of the tropical dry forest at large scales, the main objective of this thesis is to explore the use of remote sensing to assess tropical dry forest structure and diversity. Initially, the accuracy of four global and regional forest cover assessments are compared at the national level for Costa Rica and then examined in greater detail for two tropical dry forest sites in Costa Rica and Mexico. Significant errors were found systematically throughout each data set. When these errors are examined in terms of carbon sequestration forecasted over a ten-year period, the discrepancies between the maps are valued in the millions of dollars. Second, a comprehensive calibration methodology was established for leaf area index (LAI) by using a combination of litter traps, species specific leaf area values and optical estimates of LAI. In the calibration of the ground-based optical LAI estimates, it was found that the instrument underestimated the actual LAI by 40% or more in the wet season. Next, a new method of estimating LAI from satellite imagery using Bayesian Networks was explored followed by an examination of the effects of season and successional stage on forest structure and spectral vegetation indices for three Mesoamerican dry forests. Differences among the sites are attributed to both climate and varying land use and land management practices. Finally, the structure and floristic diversity of a dry forest in Costa Rica is estimated from hyperspectral satellite imagery (Hyperion). It was found that the dry season image produced the best results using a selection of wavelet decomposition coefficient elements. The final chapter summarizes the challenges for future monitoring of tropical dry forests in the context of ecological succession and remote sensing.

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LIST OF SYMBOLS AND ABBREVIATIONS

ATB	Total aboveground biomass
BN	Bayesian Network
cA_j	Wavelet decomposition approximation coefficient at level j
cD_j	Wevelet decomposition detail coefficient at level j
CDM	Clean development mechanism
CER	Certified emission reduction
C_{HCI}	Holdridge complexity index
CPT	Conditional Probability Table
D	Density of stems (No./area)
DBH	Stem diameter-at-breast-height
ERU	Emission Reduction Unit
G	Basal area (m^2/ha)
GRUAS	Set of biological corridors to be implemented into the Mesoamerican Biological Corridors
H	Canopy height (m)
H'	Shannon species richness
HCI	Holdridge complexity index
JT	Junction tree algorithm
LAI	Leaf area index, the one sided-foliage area per unit ground area)
L_e	Effective leaf area index, L_t with WAI removed
L_f	Foliar LAI
Lt	Leaf area index estimated by optical instruments (same as PAI)

MAP	Maximum posterior probability
MSR	Modified single ratio
NDVI	Normalized difference vegetation index
PAI	Plant area index
R_B	Root biomass
S	Species density (No./area)
SAVI2	Soil adjusted vegetation index 2
SLA	Specific leaf area (cm^2/g)
SR	Simple ratio
SVI	Spectral vegetation index
T-df	Tropical dry forest
WAI	Wood area index
α	Ratio of WAI to PAI
ρ_n	Near infrared reflectance
ρ_r	Red reflectance
Ω	Clumping index for foliage

Chapter 1: Introduction

1-1. Introduction

Little had changed since D.H. Janzen (1986) advocated the Costa Rican dry forest as the most threatened tropical forest type. Redford et al. (1990) showed that if species richness is the key factor for prioritizing areas for conservation, the rainforests do not hold the sole distinction of being the most species rich ecosystem. The data they present from the dry Chaco (an ecosystem comprised of grasslands, savannas, woodlands and thorn forests) in South America shows that in terms of mammal species (weighing 1kg or more), it is comparable to Manu National Park (regarded as the most species rich area in the Neotropics). Mares (1992) elaborated on these findings in a policy framework indicating that governmental policy and funding agencies may be subjected to a pre-existing bias (Redford et al. 1990) from the proponents of tropical rain forest conservation who have promoted inevitable development in other ecosystems such as the dry forest without thought about their destruction. The most popular arguments being that there is not much dry forest left and that there is far more biodiversity in the rainforests. In order to counter the loss and degradation of the dry forest, Sanchez-Azofeifa et al. (2005a) advocated a new multidisciplinary approach for conservation models that are promoted with the same enthusiasm as those from the wet forests. They also expanded on the need for adequate funding and an expansion of the scope of project designs to include comparative approaches among multiple sites within the Americas.

If the comparable species richness between these contrasting ecosystems in certain taxa is overlooked, the greater phenological diversity and higher rate of endemism (Rzedowski 1991) in the dry forests is unmistakable. For example, endemism in Mexico is estimated to be as high as 43% (Rzedowski 1991) and 73% in South American dry forests (Gentry 1995). Even on a smaller scale, such as the Chamela/Cuixmala Biosphere Reserve, endemism has been estimated to be as high as 16% (Lott 2002). Nevertheless, Sanchez-Azofeifa et al. (2005b) found that the research effort in dry forests is still 91 percentage points less than their wet counterparts, with efforts concentrated in only a few countries (Figure 1.1).

The seasonally dry tropical forest comprises nearly half of all tropical forests (Brown and Lugo as cited by Murphy & Lugo 1986). In Mesoamerica tropical dry forest ranges from the Pacific Coastal plains of Mexico and the Yucatan to the Pacific Coast of Panama covering approximately 26% of the total surface area with various deciduous vegetation types (Murphy & Lugo 1995). However, official conservation status has been awarded to less than 1 % of this area (Janzen 1988). The true extent the tropical dry forest has always been in debate and no complete estimate exists (Sanchez-Azofeifa et al. 2005b).

Sanchez-Azofeifa et al. (2005b) define the seasonally dry forest as an *area with a vegetation type dominated by deciduous trees located in an area with a mean temperature >25°C, a total annual precipitation range of 700-2000mm and three or more dry months (precipitation <100mm)*. Most woody species are drought deciduous; however, the number of species and individuals with this phenology varies with topography and successional stage. A mix of deciduous and evergreen species gives the dry forest a phenological complexity not encountered in tropical wet forests (Burnham 1997).

It is undeniable that the dry forests throughout the Neotropics have been extensively disturbed (Janzen 1988, Murphy and Lugo 1986). However, for certain areas what remains of this ecosystem is in a process of regeneration. For example, Arroyo-Mora et al. (2005) show a clear trend in the recovery of a dry forest in Costa Rica. Apart from the conservation and biodiversity aspects, avoiding or reversing undesirable changes in ecosystem processes provide a strong motivation to preserve this ecosystem. McGrady-Steed et al. (1997) show that most deterioration occurs as biodiversity declines to moderate or very low levels. However, under recuperation, ecosystem processes level off between intermediate and high levels of biodiversity and will not be affected by any further increases (McGrady-Steed et al. 1997). Therefore, not only is the prevention of functional deterioration that follows biodiversity loss a reason for conserving relatively intact ecosystems, but it is also a strong rationale for promoting the restoration of degraded ecosystems (Marks and Borman 1972, McGrady-Steed et al. 1997).

Sanchez-Azofeifa (1996) demonstrated the link between socio-economic factors and the conservation of biodiversity in Costa Rica (in terms of forest cover). The forces that drive land use/land cover change act at various scales to contribute to the conservation or degradation observed in the ecosystems (Sanchez-Azofeifa et al. 2005a,b). Without a thorough knowledge of the ecosystems being affected, it is unlikely that any sustainable development solution will be found. And without funding and research efforts being directed towards the dry forest, our knowledge of their diversity and functioning will always lag behind what is known about the rainforests.

By taking advantage of the large scale data available from satellite imagery and investigating the possibly of using these data for inferring characteristics of the dry forest, the main objective of this thesis is to explore the use of remote sensing technology to assess tropical dry forest structure and diversity. This thesis is the result of the compilation of six stand alone papers, all following the trend of conservation and monitoring of different tropical dry forest properties.

The main objectives of Chapter 2 **"Quantifying tropical forest extent and payments for environmental services from satellite imagery"** are 1) to investigate the accuracies of various global remote sensing derived land cover classification datasets of forest cover and to address the implications of their use for establishing environmental services payments baselines at the national level for Costa Rica, 2) assess how the different interpretations of the global land cover classifications affect the quantification of the value associated with environmental services in two distinct tropical dry forest environments, and 3) to under the mandate of biodiversity preservation, examine the implications of using global land cover datasets for the establishment of biological corridors.

Following the need to investigate the leaf phenology of the dry forest in greater detail, the main objective of Chapter 3 **"Calibration and assessment of seasonal changes in leaf area index of a tropical dry forest in different stages**

of succession" is to calibrate optical estimates of leaf area index (LAI) from the LAI-2000 (an optical instrument commonly used for remote measurements of LAI) using LAI derived from leaf litter data. In order to achieve that objective a thorough methodology for determining leaf area index from leaf litter data in a tropical dry forest environment is developed and as an application of the results, the seasonal variation in LAI for the three successional stages in a tropical dry forest located in Costa Rica is illustrated.

Moving to the satellite image perspective of LAI, the main objective of Chapter 4 "**Estimating leaf area index from satellite imagery using Bayesian Networks**" is to investigate a new approach for estimating an ecological variable, leaf area index, from satellite imagery using Bayesian Networks. Such models combine probability and graph theories to infer the result of complex interactions and uncertainties amongst multiple factors on specific variables of interest.

Similarly, the main objective of Chapter 5 "**Effects of season and successional stage on leaf area index and spectral vegetation indices in three Mesoamerican tropical dry forests**" is to is to evaluate seasonal Plant area index / Leaf area index and canopy openness for three sites of tropical dry forest in Mesoamerica. The role that differences in forest structure play on influencing Plant and leaf area index are also explored. Finally, regression models to estimate Plant and leaf area index from spectral vegetation indices calculated from satellite imagery and evaluated.

Addressing forest structure, biomass and diversity from the satellite image point of view, the main objective of Chapter 6 "**Ecological fingerprinting of**

ecosystem succession: estimating secondary tropical dry forest structure and diversity using Hyperion" is to address the problem of inference and mapping of tropical dry forest biophysical characteristics from hyperspectral imagery.

I finally close this thesis with a summary describing the challenges for future monitoring of tropical dry forests in the context of ecological succession and remote sensing.

1-2.References

Arroyo-Mora J.P., Sanchez-Azofeifa G.A., Rivard B., Calvo J.C., Janzen D.H. 2005. Dynamics in landscape structure and composition for the Chorotega region, Costa Rica 1960-2000. Agriculture, Ecosystems and Environment 106:27-39.

Burnham R.J. 1997. Stand characteristics and leaf litter composition of a tropical dry forest hectare in Santa Rosa National Park, Costa Rica. Biotropica 29:387-395.

Gentry A.H. 1995. Diversity and floristic composition of neotropical dry forests. In: Mooney H.A., Bullock S.H., Medina E. (Eds). Seasonally dry tropical forests, University of Cambridge Press, Cambridge. pp.146-194.

Holdridge L. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica. 206 pp.

Janzen D.H. 1986. Tropical dry forests: the most endangered major tropical ecosystem. In: Wilson E.O. (Ed) Biodiversity, National Academy Press, Washington, pp. 130-137.

Janzen D.H. 1988. Guanacaste National Park: tropical ecological and biocultural restoration. In: Carins J.J. (Ed), Rehabilitating damaged ecosystems, vol II. CRC Press, Boca Raton, FL. pp. 143-192.

Lott E. 2002. Listado floristico de Chamela. In: Noguera F.A., Vega J., García-Aldrete A., Quesada M. (Eds) Historia natural del bosque caducifolio de Chamela. Instituto de Biología, Universidad Nacional Autónoma de México. 568pp.

Mares M. 1992. Neotropical mammals and the myth of Amazonian biodiversity. Science 255: 976-979.

Marks P.L. and Borman F.H. 1972. Revegetation following forest cutting: Mechanisms for return to steady-state nutrient cycling. Science 176:914-915.

McGrady-Steed J., Harris P.M., Morin P.J. 1997. Biodiversity regulates ecosystem predictability. Nature 390:162-165.

Murphy P.G., Lugo A.E. 1986. Ecology of tropical dry forest. Annual Review of Ecology and Systematics 17:67-88

Murphy P.G., Lugo A.E. 1995. Dry forests of Central America and the Caribbean. In: Mooney H.A., Bullock S.H. (Eds) Seasonally dry tropical forests, University of Cambridge Press, Cambridge, pp.9-34.

Redford K.H., Taber A., Simonetti J.A. 1990. There is more to biodiversity then the tropical rain forests. Conservation Biology 4:328-330.

Rzedowski J. 1991. El endemismo en la flora fanerogamica mexicana: una apreciacion analitica preliminar. Acta Botanica Mexicana 15:47-64.

Sánchez-Azofeifa G.A. 1996. Assessing land use/cover change in Costa Rica, CIEDES, Universidad de Costa Rica, San Jose, Costa Rica 181pp.

Sanchez-Azofeifa G.A., Kalacska M., Quesada M., Calvo-Alvarado J.C., Nassar J.M., Rodriguez J.P. 2005a. Need for integrated research for a sustainable future in tropical dry forests. Conservation Biology 19(2):285-286.

Sánchez-Azofeifa G.A., Quesada M., Rodríguez J.P., Nassar M., Stoner K.E., Castillo A., Garvin T., Zent E.L., Calvo J.C., Kalacska M., Fajardo L., Gamon J., Cuevas-Reyes P. 2005b. Research Priorities for Neotropical Dry Forests. Biotropica 37: 477-485.

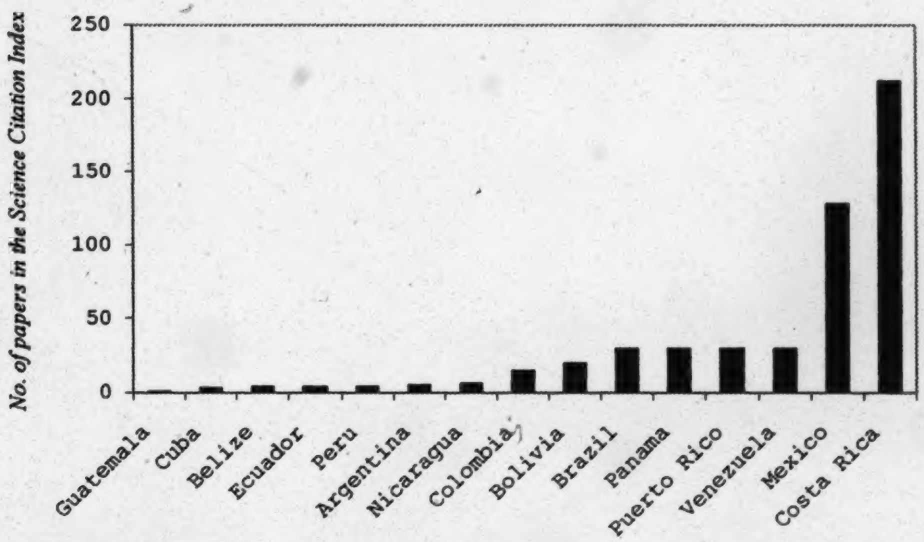

Figure 1.1. Number of Neotropical dry forest studies per country listed in the Science Citation Index for the period of 1945-2004.

Chapter 2: Quantifying tropical forest extent and payments for environmental services from satellite imagery

2-1. Introduction

In recent years, the implications of global climate change for water resources and biodiversity loss have become increasingly important for scientists, policy makers and the public alike. Elevated levels of carbon dioxide (CO_2), one of the key greenhouse gases, and possible methods of alleviating or even reversing its effects have been the topics of numerous inter-governmental panels and assessments. One possibility that has been raised to mitigate the effects of CO_2 is the concept of Certified Emission Reductions (CERs) under the Clean Development Mechanism (CDM) of the Kyoto Protocol (Pfaff et al. 2000). CERs are greenhouse gas emission reduction certificates that are obtained from permanent and temporary emission reduction projects (e.g. forestry projects) in developing countries (Olschewski and Benítez 2005). Countries that have committed to reducing greenhouse gas emissions are known as Annex B countries (mostly developed countries) each of which has a national baseline against which their progress would be measured (Busch et al. 2000).

Global fossil fuel emissions per year have been estimated by Schimel et al (2001) to be around 6.4 PgC. To counter those effects, forests may be used to sequester and store carbon for years to come. The promotion of forest regeneration and the slowing of deforestation have been proposed as such an option for Annex B countries to meet their commitments (emission levels 5% bellow 1990 level by 2008-2012). Forestry projects alone could conserve 60-87 billion tons of carbon by 2050 and reduce CO_2 in three ways: conservation, sequestration/storage and substitution (Brown 1996). Conservation policies will reduce the emissions (i.e. slow deforestation) as does sequestration /storage that result from increased forest cover and substitution will replace fossil fuel energy and products with forest biomass energy and those that store forest biomass carbon (Brown1996). Thus, one of the most important aspects of understanding and mitigating global climate change is accurately estimating carbon sequestration over large expanses of tropical forests, a problem that it is not trivial due to the lack of standardized mechanisms that can provide accurate information for different types of tropical forests (Foster et al. 2002).

Tree plantations, while needing high initial investment costs, have been shown in the literature to have extensive potential for storing carbon (Winjum et al. 1993, Sedjo 1999): an alternative to which is natural regeneration of secondary forests (Oschewski and Benitez 2005). Addressed by the Ninth Conference of the Parties, during the period up until 2012, non-permanent carbon sequestration credits may be given as temporary or long term (UNFCCC 2003). These credit certificates may be traded as a regular commodity but their initial value has been estimated to be relatively low (i.e. more supply than demand) due in part to the withdrawal of the United States from the Kyoto Protocol and the cap on Annex I countries' CDM sink projects (Den Elzen and de Moor 2003, Olschewski and Benitez 2005).

However, carbon sequestration is not the sole incentive for monitoring tropical forests. Other services within payments for environmental services include hydrological services, biodiversity services and ecosystem protection (WorldBank 2000). Currently there are payment for environmental services projects under implementation in Costa Rica, Colombia, Nicaragua and Guatemala (Pagiola 2003). There are also projects under preparation in Mexico. Venezuela, Dominican Republic, Ecuador, El Salvador and South Africa (Pagiola 2003).

Under the Ecomarkets project contract in Costa Rica, forest conservation contracts are projected at US$200/ha ($40/yr/ha), new reforestation contracts are projected at US$513/ha (reforested areas must be maintained for 15-20 years) and existing reforestation contracts from 1998 are projected at US$200/ha (Worldbank 2000). All payments are disbursed over a five-year period. Within the environmental services class carbon sequestration (the most lucrative service) is valued at US$19-US$57/ha (mean US$38) for primary and US$14.6-US$43.9 (mean US$29.4) for secondary forests (Tropical Science Centre 1999). In addition, under the Costa Rican Ministry of the Environment decree No. 32226 landowners may receive 368 Costa Rican colones per tree in agroforestry systems (MINAE 2004).

In comparison similar payments to Guatemala were estimated at $1,590/ha for reforestation, $220/ha for management and $85/ha for protection over a five year period (Juarez 2001). As of 2002 however, the structure of payments for environmental services has changed to account for services rendered by plantations and agroforestry systems (Louman and de Camino 2004).

To evaluate the effectiveness of mitigation projects in the forestry sector, three fundamental questions must be addressed: what is the **initial extent** of the forests?, what **type of forest** is there (primary, secondary)? what is the **rate of change** of the forest extent? Estimates of for payments of environmental services are greatly dependent upon the **differences** between the baseline and mitigation scenarios and on deforestation rates before and after the implementation of a project; the greater the difference the greater the estimate of carbon sequestratin/value of environmental services (Busch et al. 2000). Therefore, it is imperative to characterize the initial state and extent of the forest (baseline determination) as accurately as possible.

To accurately assess land cover changes in tropical environments at reasonable costs requires remote sensing technology. However, an initial problem in accurate estimation of forest cover is one of nomenclature. While there are numerous definitions of what is a forest (see ITTO 2002 for an in depth review), there is no consensus between the scientific community and the stakeholders. In addition, many definitions are biased towards mature wet or rain forests, neglecting seasonally deciduous forests and stages of vegetation succession. Attempts have been made to consolidate definitions with the Marrakesh Accords (UNFCCC 2001a). Based on those accords forest is defined as "*a minimum area of land of 0.05-1.0ha with tree crown cover, or equivalent stocking level, of more than 10-30% and containing trees with the potential to reach a minimum height of 2-5m at maturity*". In addition, stands temporarily below the thresholds but which are expected to grow or revert to forest are also included in the forest category

(UNFCCC 2001a). However, the definition of "forest" adopted by any one country is optional within the stated minimum levels defined by the Marrakesh Accords. In this study we adopt the Marrakesh Accord's definition of "forest" and more precisely the following refinement for a dry forest: an *area with a vegetation type dominated by deciduous trees located in an area with a mean temperature >25°C, a total annual precipitation range of 700-2000mm and three or more dry months (precipitation <100mm)* (Sanchez-Azofeifa et al. 2005)

Methods for monitoring and detecting tropical deforestation in the humid tropics have been successfully developed, tested and applied (Skole and Tucker 1993, Stone and Lefebvre 1998, Sanchez-Azofeifa et al. 2001), providing important information on the extent of tropical evergreen forests. Tropical dry deciduous forests, however have received less attention and thus the development of methods for quantifying the extent of the T-df has been neglected in comparison to wet/rain forests. Significant errors have resulted from mapping the extent of the tropical dry forest from satellite images because the cloud free images are most easily acquired during the dry season when an increased percentage of the canopy is leafless, lacking the spectral signature of green leaf biomass (Arroyo-Mora et al. 2005a). This property of the canopy induces the misinterpretation of forested areas in the image for pastures or areas with dispersed trees (Pfaff et al. 2000).

This paper investigates the implications of using various global remote sensing derived land cover classification datasets of forest cover as a **baseline scenario** at the national level for Costa Rica. We use Costa Rica as an example given its multitude of forest types and its considerable history in payment of environmental services. Subsequently, we focus specifically on the dry forest over two protected areas located in Costa Rica and Mexico and assess how the different interpretations of the global land cover classifications affect the quantification of the value associated with environmental services in this ecosystem. Finally, we address the state of the forest cover in and surrounding the GRUAS sites for each land cover classification.

2-2. Methods

2-2.1 Study areas

Our study is conducted at two levels: first, at the national level for Costa Rica and second at a specific ecosystem level (tropical dry forest) for two study sites. The country of Costa Rica (total area of 51,000km^2) is located in Central America between Nicaragua to the north and Panama to the south and the Atlantic and Pacific oceans to the east and west. Because of the central mountain range, the country encompasses numerous physiognomically different tropical forest types (life zones) (Holdridge et al. 1971). However, to facilitate the interpretation of the results and to be consistent with forest types reliably detectable from imagery we refer to two distinct forest types: predominantly evergreen (e.g. tropical wet) and predominantly deciduous (e.g. tropical dry) forest types. Subsequently, in the more detailed analysis, the two tropical dry forest areas we examine in greater detail are the Santa Rosa National Park in Costa Rica (10° 48'

53" N, 85° 36' 54" W) and the Chamela Biosphere Reserve in Mexico (19 ° 22'-19 ° 39'N, 104 ° 56'-105 ° 10' W).

Santa Rosa National Park is composed of a mixture of secondary forest in various stages of regeneration (Janzen 2000, Kalacska et al. 2004, Arroyo et al. 2005b). We refer to four stages of succession in Santa Rosa: pasture SR-P, early SR-E, intermediate SR-I and late SR-L (Table 2.1). The total study area for Santa Rosa is 500km^2. The Chamela-Cuixmala Biosphere Reserve is in the state of Jalísco, México (19 22'-19 39N, 104 56'-105 10'W). The reserve is comprised of approximately 12,600ha of forest, the majority of which has been undisturbed for hundreds of years (Maass and Martinez-Yrizar 2001). We refer to four physiognomically different forest types in and around the station. Upper ridge-top and slope (CH-U) and Lower Riparian (CH-L) forest classes are mature undisturbed forests, intermediate (CH-I) is a secondary forest stage and early (CH-E) is the first stage of regeneration populated entirely by low *Acacia* sp. bushes (Kalacska et al. 2005). The physiognomy of the different forest stages are described in Table 2.1. We included a buffer of 30km around the station for the analyses. The total study area for Chamela is 2,465km^2. In Santa Rosa there are six months of little to no precipitation and a total yearly precipitation that is highly variable (915-2558mm) (Janzen 1993). In Chamela, the precipitation ranges from 374 – 897mm with 80% falling between July and October (Maass and Martinez-Yrizar 2001). Drought deciduousness is the general leaf phenological response to the dry season (Gentry 1995, Lobo et al. 2003). Gentry

(1995) estimates that approximately 40-60% of the species in Santa Rosa are deciduous compared to over 80% in Chamela.

2-2.2 Total Aboveground Biomass

One of the most common direct methods of estimating total above ground biomass is allometric equations (Brown 2002). Site specific regression equations have been developed to estimate plant biomass (kg) from values of diameter at breast height (DBH), height and wood specific gravity (Maass et al. 2002). In other studies, general regression equations have been developed for specific forest types from DBH (Cairns et al. 2000). Carbon is assumed to be approximately 50% of the biomass (Brown 2002). The most complete estimates of carbon include not only standing live vegetation but also dead wood, root biomass and soil carbon. From forest structure data we calculated total live aboveground biomass from Brown (1997) for stems above 2.5cm DBH:

$$ATB = \exp\{-1.996+2.32(\ln D)\} \qquad (1)$$

where biomass is expressed in kilograms of dry mass and D is DBH in centimeters. Root biomass was estimated from Cairns et al. (1997):

$$R_B = \exp\{-1.0587+0.8836(\ln ATB)\} \qquad (2)$$

where ATB is aboveground tree biomass (Mg/ha). In our estimates we include only live ATB and root biomass because we do not have data regarding dead wood or soil carbon. In total, 26 plots of 20x50m were sampled in Santa Rosa and 10 of the same dimensions in Chamela; all trees above 5cm DBH were included.

2-2.3 Total Forest Cover Assessment

For Costa Rica a supervised classification map (CR2000) was produced by a combination of 14 Landsat Thematic Mapper 5 and 7 acquired in 1997 and 2000 using NASA pathfinder methodologies with a minimum mapping unit of 3ha (Sanchez-Azofeifa et al. 2001). The overall accuracy of the CR2000 data set (forest/non-forest) was estimated to be 90-92%. For the accuracy assessment, a total of 700 control points for forest with a minimum area of 3-ha and a crown closure of 80% were chosen and assessed on the ground (Sanchez-Azofeifa et al. 2001). This dataset, resampled to $1 km^2$ resolution, was used as the control in all analyses for Costa Rica.

For the Costa Rican national and the dry forest study sites' baseline determination analysis we examine three published and readily available global land cover maps created from different sensors: Global Land Cover 2000 (GLC2000) from the Canada Centre for Remote Sensing created using SPOTVEG imagery (22 classes) (Latifovic et al. 2004), IGBP from the International Geosphere Biosphere Programme created with AHVRR imagery (17 classes) (Loveland et al. 2000) and MODIS Land Cover data from Boston University (17 classes) (Muchoney et al. 2000). In addition, we include a regional land cover map, a Central American vegetation map produced by the Center for International Earth Science Information Network (CIESIN) at Columbia University for the Proyecto Ambiental Regional de Centroamerica (PROARCA) created from AVHRR imagery (17 classes) (CCAD et al. 1998) for Costa Rica only (i.e. data not available for the dry forest site in Chamela Mexico).

As the control data for Chamela Mexico a supervised classification map (MX2003) from a regional classification using the ASTER sensor (resampled to 1 km^2 resolution) for the year 2003 (Sanchez-Azofeifa and Quesada unpublished) is used.

2-3. Results

2-3.1 Forest cover estimation at the national level for Costa Rica

The overall forest cover estimates for Costa Rica from the different land cover maps are shown in Figure 2.1. In comparison to the CR2000 data, each land cover map underestimates the actual forest cover for the predominantly deciduous (dry) ecosystem (Figure 2.1f). The area demarcated as "dry" in Figure 2.1f is predominantly deciduous or contains trees that are facultatively deciduous during harsh dry seasons (periods of little to no rainfall). This area encompasses 14% of Costa Rica (7,140km^2). For the evergreen vegetation, in general, in comparison to the CR2000 dataset, in forest extent is reasonably close except for the overestimation of the forest in the northeastern and central sectors of the country because of the inclusion of known palm, coffee, pineapple, yucca and other plantations in the forest cover class. The overall forest accuracies for GLC2000 (74%) and MODIS (76%) (Table 2.2) reflect the high prevalence and accuracy of "forest" for the majority of the evergreen forest areas in the country (Figure 2.1) (e.g. 79% - GLC2000 and 88% - MODIS) (Table 2.2). However, the low non-forest accuracies (e.g. 32% and 16% for GLC2000 and MODIS respectively) for all land cover maps indicate an overestimation of the forest in the evergreen forest areas (Table 2.2). The poor accuracies for all datasets over the deciduous forest areas (36% mean accuracy for all datasets) indicate a severe underestimation of the deciduous forest (Table 2.2). Table 2.3 indicates the total forest area from the land cover maps, along with the results from a published additional study (Mayaux et al. 1998) in comparison to the CR2000 dataset. Every land cover map overestimates the extent of the forest by as much as 16,000km^2 with the exception of Mayaux et al. (1998) who underestimate the forest cover by 9,777km^2. PROARCA is the closest in the overall estimate for forest area with 27,792km^2 which is only 4,565km^2 more than the CR2000 dataset. The MODIS land cover dataset is the farthest from CR2000 at 39,409km^2.

2-3.2 Tropical dry forest sites

The total forest area from the CR2000 data set for Santa Rosa is 276.6km^2. For Chamela the MX2002 reveals 1925.6km^2 of forest as control. The range of land cover classes (and forest/non-forest accuracies) found in the dry deciduous study areas based on the four global/regional land cover data sets is illustrated in Table 2.4. The consensus for the dominant class in Santa Rosa from the land cover maps is "cropland" or "agriculture", with the forest classes being minimal in comparison. However, from the CR2000 data for Santa Rosa, the dominant class is "forest" with an actual coverage of 55%. The actual forest cover for Santa Rosa has also been reported by an independent study from Arroyo-Mora et al. (2005b). Every land cover map underestimated the total forest in Santa Rosa by 130.6km^2(MODIS) to 196.8km^2 (PROARCA) in comparison to CR2000. The highest accuracy is from both the PROARCA and MODIS data sets for forest at

34% (non-forest accuracies of 92% and 48% respectively, Table 2.2). The lowest accuracy is from GLC2000 at 16% for forest (78% non-forest).

For Chamela the dominant class from the land cover maps is cropland (GLC2000), mixed forest (MODIS) or evergreen broadleaf forest (IGBP) (Table 2.4). From the MX2002 database, the dominant class is forest with an extent of 78% (1925.6km^2). With all forest classes combined, for total extent, MODIS was very close at 79% (1950.3km^2) followed by IGBP at 70% (1728km^2) and GLC2000 at 46% (1135.6km^2). The highest accuracy for forest cover was from MODIS at 66% (non-forest accuracy 37%) indicating that while the amount of forest is close to the MX2002 dataset, the precision (actual location) of the forest is incorrect (Table 2.2). The lowest forest accuracy was from the GLC2002 data set for forest (41%) with a non –forest accuracy of 42%. For all the land cover maps forest classes were assigned based on descriptions as well as nomenclature. For example, the classes such as "woody savannah" because of the description were also included in the forest classes along with those that were labeled "forest".

2-3.3 Environmental Services Payments: Forecasted Carbon sequestration

Arroyo-Mora et al. (2005a) found a rate of change of +4.91% per year in forest cover for the period of 1986-2000 in a larger dry forest area encompassing the Santa Rosa study area. Assuming the same constant rate of change in forest cover for the 2000-2010 period, Table 2.5 and Figure 2.2 illustrate the forecasted total forest area for each land cover map taking the results from this study as the year 2000 baseline for each. The CR2000 dataset shows a total increase in forest cover by 2010 of 170km^2 followed most closely by MODIS at 89.8km^2 and with the greatest difference, PROARCA at 49km^2. With the assumption that ratio of forest stage (i.e. early:22%, intermediate:47%, late:31%) found in the area by Arroyo-Mora et al. (2005b) remains relatively constant, and the values of MgC/ha/stage from Table 2.1 are used, the carbon gains forecasted by each data set are shown in Table 2.5. The greatest carbon gain is from the CR2000 dataset with a total of 1,074,691MgC followed by MODIS with a total of 567,107MgC and with the greatest difference, PROARCA at 310,207MgC. If successional stages are disregarded and an average value of 91.32MgC/ha is used (Kauffman et al. unpublished), 1,553,401MgC are the forecasted gain from CR2000 in comparison to 819,720MgC (MODIS) or 448,386MgC (PROARCA) (Table 2.5). As can be seen in Figure 2.2, the rate of change of the forest cover is much lower for all land cover maps in comparison to CR2000 and each year the difference is compounded. An unprecedented and unrealistic rate of change would be needed by models incorporating any of the land cover maps to reach the same final forecasted value of total forest area as shown by CR2000.

From the projected increase in forest cover (2000-2010), the estimated value of carbon sequestration from the CR2000 dataset is $US 500,109 ($US29.4/ha) with a range of $US 248,354-746,762 ($US 14.6-43.9) (Figure 2.3). The MODIS land cover map is the closest in its projection with a projected value of carbon sequestration in 2010 at $US 263,904 and a range of $US 131,055-394,061 (Figure 2.3).

2-3.4 Biological Corridors and the Protection of Biodiversity

Under the mandate of biodiversity protection within the environmental services payment projects other related uses of remotely generated forest cover data such as the planning and assessment of national parks and protected areas must also be taken into consideration. With the current national parks, all land cover maps estimated the true extent of the forest with reasonable accuracy (Table 2.4). However, this observation does not hold if the proposed biological corridors are examined (Table 2.4). The majority of the area covered by the GRUAS corridors (proposed biological corridors within Costa Rica to be integrated into the Mesoamerican biological corridor program) is within the primarily evergreen forest (Figures 2.1 and 2.4). Erroneous forest cover estimates within these GRUAS corridors could potentially overestimate the actual forest extent and lead to a misplacement of the protected areas. The effects of inflated total forest accuracies in baseline scenarios (Table 2.3) due to an overestimation of forest in areas covered by an evergreen canopy coupled with an underestimation of forest with a deciduous canopy may lead to the establishment of such protected corridors in areas that are not under the greatest deforestation pressures and whose effects may therefore, not be the most productive. In addition to deforestation pressure, the concentration of most monitoring/conservation systems in the evergreen forest is evident when it is considered that only two of the 36 GRUAS corridors and four of the protected areas are in the deciduous forest. Pfaff and Sanchez-Azofeifa (2004) have shown how areas should be prioritized based on an index of deforestation pressure and Van Laake and Sanchez-Azofeifa (2004) stated that deforestation must be expressed as an instantaneous localized process rather than a function derived over a large area that is not sensitive enough for local or regional changes. However, in order to apply either the deforestation pressure methodology or the localization of deforestation hot spot methodology, spatially reliable estimates of deforestation are needed; the basic requirement for which is an **accurate baseline** forest cover maps from which to begin modeling.

2-4. Discussion and Conclusion

While this study is not meant to forecast an overly negative shadow on the use of remotely sensed data, it does intend to show the type of caution that must be used when selecting the appropriate data sources for analyses. Imagery, preferably medium resolution (i.e. 30m), should be acquired for each study site/region where environmental services payments projects are projected to be set-up. The subsequent classification of the imagery to establish the baseline would then be specific to the area and validation should also be done with the unique characteristics of the region in mind. Used with caution, remotely sensed data is a powerful tool for providing information to decision makers, the study of land use-ecosystem interactions and the regional application of integrated models.

Many previous studies have examined the inconsistencies between forest cover data sets (e.g. Mayaux et al. 1998, Kleinn et al. 2002, Kerr et al. 2001). It is important to acknowledge this because there are several problems with accuracy, under estimation, over estimation and misclassification of forest cover. However, there is a need to move beyond examining accuracies and to begin examining their implications which can be in many cases greater than differences in a simple measure of forest extent. With the need for reliable forest cover estimates for establishing baselines, erroneous estimates could force trading to increase global net emissions and any mitigation projects would be both misdirected and inefficient (Kerr et al. 2002). This incompatibility between maps will end up costing millions of misspent dollars over time.

For a project to be eligible for Emission Reduction Units (ERUs) under the United Nation's Framework Convention on Climate Change (UNFCCC) in the Land Use Change and Forestry (LUCF) category it has to show a successful accumulation of sequestered carbon (Trines 1998). The project must report the size of the carbon pools forming part of the project as well as any changes to the sizes of the pools (Trines 1998). The only way a project can claim ERUs or credits through the CDM, is if it can show a greater sequestration of carbon than the baseline scenario. Any erroneous estimates of either the initial forest cover or change (i.e. deforestation rate) would lead to diverse and unrealistic values for the carbon stocks.

For the tropical dry forest specifically, the forest identified in the wet season images (November in Santa Rosa and August in Chamela) is a mixture of both deciduous and semi-evergreen species as well as pasture lands with enough green herbaceous biomass to produce a spectral signature comparable to trees (Figure 2.5). In comparison, the forest area extracted from the dry season (April in Santa Rosa, March in Chamela) images may be comprised of similar or overlapping species, but located in areas where the microclimate enables them to retain their foliage along with species that practice inverse phenology. Kalacska et al. (2004, 2005) have shown that the areas in Santa Rosa that predominantly retain partial foliage in the dry season are found in the late successional stage. In Chamela, however, the lower Riparian forest (CH-L) has a different species composition (i.e. more semi-evergreen species) and very different microclimate (Quesada, unpublished observation). Yet, the other late stage (CH-U) is almost entirely deciduous in the dry season. When the majority of the trees are without foliage, the spectral signature is comprised of a mixture from soil, leaf litter, rock, bark. etc., rather than predominantly green leaves (Figure 2.5). In general, a higher accuracy for the non-forest classes compared to the forest classes can be seen for every classification and land cover map except for the wet season image classifications. For Santa Rosa the reason the land cover maps have the large discrepancy between the accuracies of the two classes is that the majority of the area is classified as non forest. Therefore, the chance that a "forest" control point will fall into a pixel classified as forest is much less than the chance a "non forest" control point will fall into a pixel classified as non forest. This is the same for the dry season image classifications. The accuracy of the wet season image classifications is better in the forest class than the non forest class because these techniques overestimate the total extent of forest. This overestimation is in large part due to pastures in the wet season that contain high green biomass and thus, their spectral signature resembles that of forest stands (Figure 2.5). For Chamela, The location of the forest is incorrect (i.e. low accuracy) while the extent (i.e. total area) is generally close to what can be found on the ground. Thus, the application of inappropriate classification technique will also result in large discrepancies. Methods must be flexible and may not all be used on an operational mapping project without extensive ground truth information. In addition, calibration or validation of large scale maps without consideration of the ecological characteristics specific to each environment may contribute to the errors.

A common assumption is that at the spatial resolution of most global land cover maps (1km^2) the majority of the pixels is not homogenous in the land cover class they represent and therefore, under and/or over estimation of various classes is accepted. For the dry deciduous forest in Costa Rica Arroyo-Mora et al. (2005a) found that the mean patch size of forest was 1.07km^2. In addition the forest patches are in general comparable in size or in some cases larger than the agriculture patches (i.e. dominant class in the land cover maps) (Table 2.4). These results indicate that although there may be many "mixed 1km^2 pixels" there are still a sufficient number of "primarily forest pixels" in order for the deciduous forest to be present and included on land cover maps.

Based on examinations of socioeconomic pressures it has been stated that research should focus in the wet forest life zones (Kerr et al. 2004). In Costa Rica with the collapse of the beef industry and the short utility of tropical wet forest soils for agriculture, there are significant deforestation pressures in the wet forest life zones (Sanchez-Azofeifa et al. 2001). However, we argue that similar if not greater pressures also exist in the dry forest, compounded by the fact that they are practically non existent in global land cover classifications. Due to low biotic and abiotic stresses and a comfortable climate, the dry forest has always been the preferred ecosystem for human settlement and animal husbandry (Ewel 1999). The dry forest is globally extensive (42% of tropical forests are dry) but because of its appeal to human settlement it is also among the least protected (Murphy and Lugo 1986). In Mesoamerica only 0.09% has official conservation status, and only 2% is in large enough patches to attract the attention of conservation organizations (Janzen 1988). Pfaff and Sanchez-Azofeifa (2004) also illustrate large areas in the dry deciduous forest in Costa Rica that are under a high pressure of deforestation. This along with the need to acknowledge their existence/location and the phenological complication accounting for the problems associated with estimating their true extent should make them a priority in global environmental services payments and carbon mitigation projects.

In addition, the following example from Chamela illustrates the other potential problems that can arise from using various estimates of forest cover. The land tenure system around Chamela favours subsistence and commercial crops, tourism and cattle grazing. And presently the land is most valued for tourism rather than any other land use, including forest (Maass et al. 2005). However, the short term return of such land uses does not make up for the long term cost associated with these practices. For example, the clearing of the forests could result in either a scenario where certain pollinators will have to be brought to the area for various crops (which are of considerable value) or a scenario which could result in the loss of hundreds of thousands of dollars worth of crops (Maass et al. 2005). Either of these two scenarios would be a very expensive endeavour compared to leaving forest and utilizing the various services it would provide. If the maps being used by decision makers do not show the true extent of the forest, possible mechanisms for its protection will not even be considered.

A final broad question that must be considered concerns both the utility and facility of using remotely sensed data for payment of environmental services projects in general. Rosenqvist et al. (2003) review the possible functions of remote sensing technology as part of decision support systems for the Kyoto Protocol. Two specific points from their review require special consideration for the use of remotely sensed data. First, the definition of "forest" from the Marrakesh Accords (UNFCCC 2001a) as referred to earlier. Second, based on the Bonn Agreements all forest and aforestation/ reforestation/deforestation activities are defined based on land use rather than land cover (UNFCCC 2001b). The implications of this are such that an area of cleared land that is expected to return to forest will still be counted as forest under the Kyoto protocol and will not count as deforestation (Rosenqvist et al. 2003). In addition, only direct-human induced aforestation/reforestation/deforestation events will be considered. Thus, once a reliable land cover map of forest and non forest areas is produced it must further be subject to additional in situ verification for land use classification.

We have shown that depending on which study is used, the estimations of environmental services payments, carbon content and the accuracy of the forest cover will vary accordingly. Until questions regarding nomenclature and types of forest classes are resolved, even for the simplest questions of "how much forest is there?" and "where is the forest?" discrepancies between various studies and problems with the estimations of payments of environmental services will persist.

These discrepancies may end up costing hundreds of millions of dollars in erroneous payments and unsuccessful carbon mitigation projects as well as the irrevocable loss of biodiversity. In order to rectify the discrepancies. more rigorous methods including a greater emphasis on the collection of ground control data are required. In addition a standardized description of the "forest" class which takes into account the heterogeneity of the deciduous dry forests as well as every class included in a land cover analysis would reduce the uncertainty associated with the current land cover classifications. Some large scale global land cover maps are inherently unrealistic when examined closely at the ecosystem or country scales. The implications of our study present a need for looking beyond simple accuracy assessments of these products and examining them in broader contexts such as environmental services payments and the establishment of biological corridors at national and regional scales.

Fassnacht et al. (2005) identify the importance of understanding the limitations and caveats associated with using products created from remotely sensed data. The four key issues they identify are differences in direct and indirect models, difference between class-based and continuous mapping models, scale and accuracy assessment. Similar issues illustrated in this study strengthen the need for a stronger awareness about how maps created from imagery should be used and the technical limitations associated with such data. Nevertheless there is no doubt that remote sensing is a powerful tool for policy makers when used appropriately.

2-5. References

Arroyo-Mora J.P., Sanchez-Azofeifa G.A, Rivard B., Calvo J.C., Janzen D.H. (2005a) Dynamics in landscape structure and composition for the Chorotega region, Costa Rica from 1960 to 2000. *Agriculture Ecosystems and Environment* **106**: 27-39.

Arroyo-Mora J.P., Sanchez-Azofeifa G.A., Kalacska M., Rivard B., Calvo-Alvarado J.C., Janzen D.(2005b) Secondary forest detection in a Neotropical dry forest using Landsat 7 ETM+ and IKONOS imagery. *Biotropica* **37:** 497-507.

Brown S.(2002) Measuring, monitoring and verification of carbon benefits for forest-based projects. *Philosophical Transactions of the Royal Society of London A* **360** 1669-1683.

Brown S. (1997) Estimating biomass and biomass change of tropical forests: a primer. Rome, FAO Forestry Paper no. 143.

Brown S.(1996) Mitigation potential of carbon dioxide emissions by management of forests in Asia. *Ambio* **25** 273-278.

Busch C.B., Sathaye J.A., and Sanchez-Azofeifa G.A. Estimating the greenhouse gas benefits of forestry projects: a Costa Rican case study. (2000) Berkeley, CA, Ernest Orlando Lawrence Berkeley National Laboratory.

Cairns MA, Brown S, Helmer EH, Baumgardner GA(1997) Root biomass allocation in the world's upland forests. *Oecologia* **111** 1-11.

Cairns MA, Haggerty P.K., Alvarez R, De Jong BHJ, Olmsted I (2000) Tropical Mexico's recent land-use change: A region's contribution to the global carbon cycle. *Ecological Applications* **10** 1426-1441.

CCAD. (1998)Central America Vegetation/Land Cover Classification and Conservation Status (PROARCA) . Central American Commission on Environment and Development (CCAD), U. S., Agency for International Development (USAID), International Resources, Group, Ltd. IRG The Nature Conservancy TNC and Winrock International, and (WI). Palisades NY, CIESIN.

Den Elzen M.G.J., de Moor A.P.G.(2002) Analyzing the Kyoto Protocol under the Marrakesh Accords: economic efficiency and environmental effectiveness, *Ecological Economics* **43**: 141–158.

Ewel JJ(1999) Natural systems as models for the design of sustainable systems of land use. *Agroforestry Systems* **45** 1-21.

Fassnacht K.S., Cohen W.B., Spies T.A. (2005) Key issues in making and using satellite-based maps in ecology: A primer. *Forest Ecology and Management* In press.

Foster JR, Kingdon CC, Townsend PA(2002) Predicting tropical forest carbon from EO-1 hyperspectral imagery in Noel Kempff Mercado National Park, Bolivia. *IEEE* 3108-31110.

Gentry A.H. (1995) Diversity of floristic composition of Neotropical dry forests. In:Seasonally dry tropical forests (eds Mooney S.H., Bullock S.H., Medina E.), pp. 146-194. Cambridge University Press, Cambridge, UK.

Holdridge L.R., Grenke W.C., Hatheway W.H., Liang T., Tosi J. Jr. (1971) Forest Environments in Tropical Life Zones: A Pilot Study. Pergamon Press, New York.

ITTO. ITTO guidelines for the restoration, management and rehabilitation of degraded and secondary tropical forests. (2002) Yokohama, Japan, ITTO. Policy Development Series 13.

Janzen D.H. (1993) Caterpillar seasonality in a Costa Rican dry forest. In:Caterpillars: Ecological and evolutionary constraints on foraging (eds Stamp N.E., Casey T.M.), pp. 448-477. Chapman Hill, New York.

Janzen D.H.(2000) Costa Rica's Area de Conservacion Guanacaste: a long march to survival through non-damaging biodevelopment. *Biodiversity* **1** 7-20.

Janzen, D.H.(1988) Guanacaste National Park: tropical ecological and biocultural restoration. In: Cairns, J.J. (Ed.), Rehabilitating Damaged Ecosystems, vol. II. CRC Press, Boca Raton, FL, pp. 143-192.

Juarez M.A. (2001) Estado actual del manejo forestal en Guatemala. Proyecto Information y Analisis para el Manejo Forestal Sostenible: integrando esfuerzos nacionales e internacionales en 13 paises tropicales en America Latina (GCP/RLA/133/EC). http://www.rlc.fao.org/proyecto/rla133ec/MF-pdf/MF%20-%20Guatemala.PDF . FAO, Santiago Chile. 17.

Kalacska M., Sanchez-Azofeifa G.A., Calvo-Alvarado J.C., Rivard B., Quesada M.(2005) Effects of season and successional stage on leaf area index and spectral vegetation indices in three Mesoamerican tropical dry forests. *Biotropica* **37**:486-496.

Kalacska M., Sanchez-Azofeifa G.A., Calvo-Alvarado J.C., Rivard B., Quesada M., Janzen D.H.(2004) Species composition, similarity and diversity in three successional stages of tropical dry forest. *Forest Ecology and Management* **200** 227-247

Kerr S., Hendy J., Liu S., and Pfaff A.S.P. (2004) Tropical forest protection, uncertainty, and the environmental integrity of carbon mitigation policies. MOTU Economic and Public Policy Research.

Kerr S, Pfaff ASP, and Sanchez A. (2002) The dynamics of deforestation: evidence from Costa Rica. MOTU Economic and Public Policy Research.

Kerr S, Pfaff ASP, Sanchez A, and Boscolo M. (2001) How can carbon sequestration in tropical forests rewarded? Evidence from Costa Rica. (ed Panayotou T.) Central America Project, Environment: Conservation and Competitiveness. Harvard Institute for International Development.

Kishor N.M. and Constantino L.F. (1993) Forest management and competing land uses: an economic analysis for Costa Rica. Washington D.C., World Bank, Latin American Technical Department, Environmental Division.

Kleinn C., Corrales L., Morales D.(2002) Forest area in Costa Rica: A comparative study of tropical forest cover estimates over time. *Environmental Monitoring and Assessment* **73** 17-40.

Latifovic R., Olthof I.(2004) Accuracy assessment using sub-pixel fractional error matrices of global land cover products derived from satellite data. *Remote Sensing of Environment* **90** 153-165.

Lobo J.A., Quesada M., Stoner K.E., Fuchs E.J., Herrerias-Diego Y., Rojas-Sandoval J., Saborio-Rodriguez G.(2003) Factors affecting phenological patterns of Bombacaceous trees in seasonal forests in Costa Rica and Mexico. *American Journal of Botany* **90** 1054-1063.

Louman B., and de Camino R. (2004) Aspectos generales. In:Planificacion del manejo diversificado de bosques latifoliados humedos tropicales pp. 1-54. CATIE, Turrialba, Costa Rica.

Loveland TR, Reed BC, Brown JF, Olhen DO, Zhu Z, Yang L, Merchant JW(2000) Development of a global land cover characteristics database and IGBP DISCover from 1 km AVHRR data. *International Journal of Remote Sensing* **21** 1303-1330.

Maass J, Balvanera P, Castillo A, DailyGC, Mooney HA, Ehrlich P, Quesada M, Miranda A, Jaramillo VJ , García-Oliva F, Martínez-Yrizar A, Cotler H, López-Blanco J, Pérez-Jiménez A, Búrquez A, Tinoco C, Ceballos G, Barraza L, Ayala R, Sarukhán J(2005) Ecosystem services of tropical dry forests: insights from long-term ecological and social research on the Pacific Coast of Mexico. *Ecology and Society* **10** online http://www.ecologyandsociety.org/vol10/iss1/art17/.

Maass JM, Martinez-Yrizar A, Patino C, Sarukhan J(2002) Distribution and annual net accumulation of above-ground dead phytomass and its influence on throughfall quality in a Mexican tropical deciduous forest ecosystem. *Journal of Tropical Ecology* **18** 821-834.

Maass M. and Martinez-Yrizar A. (2001) NPP Tropical Forest: Chamela, Mexico, 1982-1995. Oak Ridge Tennessee, Oak Ridge National Laboratory Distributed Active Archive Center.

Mayaux P., Achard F., Malingreau J.-P.(1998) Global tropical forest area measurements derived from coarse resolution satellite imagery: a comparison with other approaches. *Environmental Conservation* **25** 37-52.

MINAE (2004) Costa Rican Minister of the Environment, Ministerial decree No. 32226. San Jose, Costa Rica.

Muchoney D, Borak J, Chi H, Friedl M, Gopal S, Hodges J, Morrow N, Strahler A(2000) Application of the MODIS global supervised classification model to vegetation and land cover mapping of Central America. *International Journal of Remote Sensing* **21** 1115-1138.

Murphy PG. Lugo AE. (1986) Structure and biomass of a subtropical dry forest in Puerto Rico. *Biotropica* **18** 89-96.

Olschewski R., Benítez P.C. (2005). Secondary forests as carbon sinks? The economic impact of accounting methods on reforestation projects in the tropics. *Ecological Economics* **55**: 380-394.

Pagiola S. (2003). Selling Environmental Services to Help Finance Reforestation. Symposium on Financing Reforestation in LatinAmerica. Panama City, Panama. November 21, 2003. Available online: http:// research.yale.edu/prorena/documentos/IIIer_encuentro_presentacion_pagiola.pdf

Pfaff A.S.P., Kerr S., Hughes R.F., Liu S., Sanchez-Azofeifa G.A., Schimel D., Tosi J., Watson V.(2000) The Kyoto protocol and payments for tropical forests: An interdisciplinary method for estimating carbon-offset supply and increasing the feasibility of a carbon market under the CDM. *Ecological Economics* **35** 203-221.

Pfaff A.S.P., Sanchez-Azofeifa G.A.(2004) Deforestation pressure and biological reserve planning: a conceptual approach and an illustrative application for Costa Rica. *Resource and Energy Economics* **26** 237-254.

Rosenqvist A, Milne A, Lucas R, Imhoff M, Dobson C(2003) A review of remote sensing technology in support of the Kyoto Protocol . *Environmental Science and Policy* **6** 441-455.

Sanchez-Azofeifa G.A., Daily G.c., Pfaff A.S.P., Busch C. (2003). Integrity and isolation of Costa Rica's national parks and biological reserves: examining the dynamics of land-cover change. Biological Conservation **109**: 123-135.

Sanchez-Azofeifa G.A., Harriss R.C., Skole D.L.(2001) Deforestation in Costa Rica: A quantitative analysis using remote sensing imagery. *Biotropica* **33:** 378-384.

Sánchez-Azofeifa G.A., Quesada M., Rodríguez J.P., Nassar M., Stoner K.E., Castillo A., Garvin T., Zent E.L., Calvo J.C., Kalacska M., Fajardo L., Gamon J., Cuevas-Reyes P. (2005) Research Priorities for Neotropical Dry Forests.

Biotropica **37**: 477-485.

Schimel D. S., Ciasis P., Peylin P., Braswell B.H., Apps M.J., Baker D., Bondeau A., Canadell J., Churkina G., Cramer W., Denning A.S., Field C.B., Friedlingstein P., Goodale C., Heinmann M., Houghton R.A., Melillo J.M., Moore III B., Murdiyarso D., Noble I., Pacala S.W., Prentice I.C., Raupach M.R., Rayner P.J., Scholes R.J., Steffen W.L., Wirth C., House J.I., Hibbard K. A., and Bousquet P. (2001) Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature* **414:** 169-172.

Sedjo R.A., Wisniewski J., Sample A.V., Kinsman J.D. (1995) The economics of managing carbon via forestry: assessment of existing studies. *Environmental and Resource Economics* **6**: 139–165.

Skole D, Tucker C(1993) Tropical deforestation and habitat fragmentation in the Amazon - satellite data from 1978 to 1988. *Science* **260:** 1909.

Stone T.A., Lefebvre P.(1998) Using multi-temporal satellite data to evaluate selective logging in Para, Brazil . *International Journal of Remote Sensing* **19** 2517-2526.

Trines E. (1998) Assessing and monitoring carbon offset projects: the Costa Rican case. *Commonwealth Forestry Review* **77:** 214-218.

UNFCCC (2003) Modalities and procedures for afforestation and reforestation project activities under the clean development mechanism in the first commitment period of the Kyoto Protocol. Decision-/CP.9 Available at: www.unfccc.int.

UNFCCC. (2001a) The Marrakesh Accords and the Marrakesh Declaration. Proceedings of the Seventh Conference of the Parties (COP 7). FCCC/CP/2001/13/Add.1 (Annex, Section A).

UNFCCC. (2001b) Report of the Conference of the Parties of the Second Part of its Sixth Session held at Bonn from 16 to 27 of July 2001 (COP 6, Part 2). FCCC/CP/2001/5 (Annex, Section VII).

Van Laake P., Sanchez-Azofeifa G.A. (2004). Focus on deforestation: zooming in on hot spots in highly fragmented ecosystems in Costa Rica. Agriculture, *Ecosystems and Environment* **102**: 3-15.

Winjum J.K., Dixon R.K., Schroeder P.E.(1993) Forest management and carbon storage: an analysis of 12 key forest nations, *Water, Air and Soil Pollution* **70**: 239–257.

World Bank. (2000). Project Appraisal Document on a Proposed IBRD Loan of US$3.6Millon to the republic of Costa Rica and a Grant from the Global Environment Facility Trust Fund of SDR 6.1 Million (US$8 Million Equivalent) to the National Forestry Financing Fund for the Ecomarkets Project. May 15,

2000. Report No: 20434-CR. Available online at: http://www-wds.worldbank.org/servlet/WDS_IBank_Servlet?pcont=details&eid=000094946_00052605361222

Table 2.1 Forest structure characteristics and allometric Carbon (C) content from live total above ground and root biomass for all stages of forest in Santa Rosa and Chamela.

Forest stage[‡]	Canopy height (m)	Basal area (m^2/ha)	Stem density	Species density	No. strata	C (tons/ha)
SR-P	2±0.5	0±0.0	0±0	1±0	0	-
SR-E	7.5±2.2	11.7±5.4	112±64	15±7	1	31.8±1.8
SR-I	10.3±3.4	21.4±6.8	130±35	29±5	1	60.9±2.5
SR-L	15.0±2.2	30.1±6.5	107±42	29±7	2	88.9±2.0
CH-E	1.3±0.4	0±0.0	0±0	1±0	0	-
CH-I	11.0±2.2	10.4±4.7	146±103	8±6	1	22.4±2.3
CH-U	8.9±1.8	13.2±2.5	181±5	31±12	1	29.5±3.0
CH-L	21.1±1.0	25.8±2.6	124±10	31±4	2	72.6±3.4

[‡] Forest structure data for Santa Rosa are from Kalacska et al. (2004) and Arroyo-Mora et al. (2005.) and from Kalacska et al. (2005.) for Chamela. Census includes only woody stems with a DBH ≥ 5cm. Canopy height for SR-P reflects height of African grass *Hyparrhenia rufa* (Jaragua) during the wet season. For CH-E it reflects the height of the *Acacia* sp. bushes.

Table 2.2. Forest and Non-forest accuracies (%) for the national level analysis for Costa Rica and the two tropical dry forest sites (Santa Rosa and Chamela)

Accuracy	GLC2000	MODIS	IGBP	PROARCA	*Mean*
Costa Rica Predominantly deciduous	56	35	18	36	*36*
Costa Rica Predominantly evergreen	79	88	70	73	*78*
Costa Rica Overall Forest	74	76	59	64	*68*
Costa Rica Overall Non-forest	32	16	32	59	*35*
Santa Rosa Forest	16	34	24	34	*27*
Santa Rosa Non-forest	78	48	72	92	*73*
Chamela Forest	41	66	61	-	*56*
Chamela Non-forest	42	37	38	-	*39*

Table 2.3 Total forest cover for Costa Rica and the National Parks and GRUAS corridors in Costa Rica for each data set. CR2000 control dataset is shown in italics.

Land Cover Map	Total forest area (km^2)	National Parks (km^2)	GRUAS (km^2)
MODIS	39,409	4,484	5,414
GLC2000	36,961	4,719	4,873
IGBP	32,648	4,311	5,102
PROARCA	27,792	4,642	3,621
CR2000	*23,227*	*5,054*	*3,480*
Mayaux et al. 1998	13,450	N/A	N/A

Table 2.4 Forest and Non-forest classes from the land cover maps for Santa Rosa and Chamela. PROARCA is only available for Santa Rosa.

Location	Land cover map	No. forest classes (extent)	Dominant class (extent)	2nd dominant class (extent)	Other classes
Santa Rosa	GLC2000	6 (26%)	Cropland (70.1%)	Tropical Broadleaved Evergreen forest – Open Canopy at (19%)	Grassland, water
Chamela	GLC2000	6 (46.4%)	Cropland (50.6%)	Tropical Broadleaved Evergreen Forest – Closed Canopy (28.8%)	Grassland, water, consolidated rock with sparse vegetation
Santa Rosa	IGBP	5 (14.3%)	Cropland (51.2%)	Cropland – natural vegetation mosaic (14.7%)	Savannah, grassland
Chamela	IGBP	5 (70.1%)	Evergreen Broadleaved Forest (26.7%)	Cropland (25%)	Savannah, grassland
Santa Rosa	MODIS	5 (35%)	Cropland (64.8%)	Woody savannah (2.3%)	Shrubland, savannah, grassland, cropland/natural veg. mosaic
Chamela	MODIS	5 (79.1%)	Mixed forest (29%)	Evergreen broadleaf forest (28.3%)	Shrubland, savannah, grassland, cropland, cropland/natural veg.mosaic
Santa Rosa	PROARCA	7 (21.9%)	Agriculture (72%)	Tropical Broadleaf deciduous woodland (7.2%)	Tropical perennial graminoid grassland, forest-woodland-agriculture complex, urban-veg. complex, agriculture and urban-industrial

Table 2.5 Initial and 10yr forecasted total forest cover and Carbon gain (assuming a +4.91% increase in forest cover per year) for the Santa Rosa dry forest study area (total area 500km^2)

	CR2000	GLC2000	IGBP	MODIS	PROARCA
Initial forest cover (km^2)	276.6	128.3	137.6	146.0	79.8
10yr forecasted forest cover (km^2)	446.7	207.2	222.2	235.7	128.9
Change in forest cover (km^2)	170.1	78.9	84.6	89.8	49.1
Total Carbon gain MgC (allometric with stages from Table 2.1)	1,074,691	498,492	534,626	567,107	310,207
Total Carbon gain MgC (average 91.32MgC/ha)	1,553,401	720,540	772,769	819,720	448,386

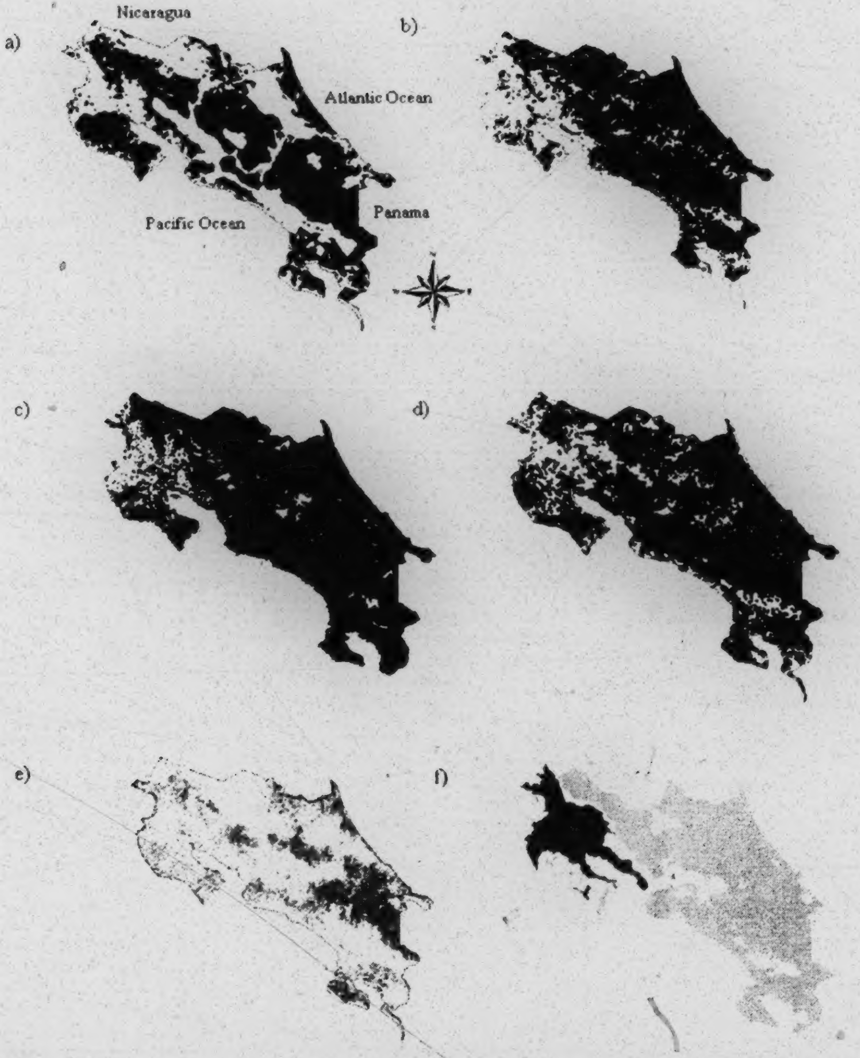
a)
Nicaragua
b)
Atlantic Ocean
Panama
Pacific Ocean
c)
d)
e)
f)

Figure 2.1 Total forest cover extracted for Costa Rica from the various global/regional land cover maps. a) PROARCA b) IGBP c) MODIS d) GLC2000 e) CR2000 f) areas comprised of a dry season deciduous canopy (dark grey) and areas with a predominantly evergreen canopy (medium grey) in Costa Rica (light grey).

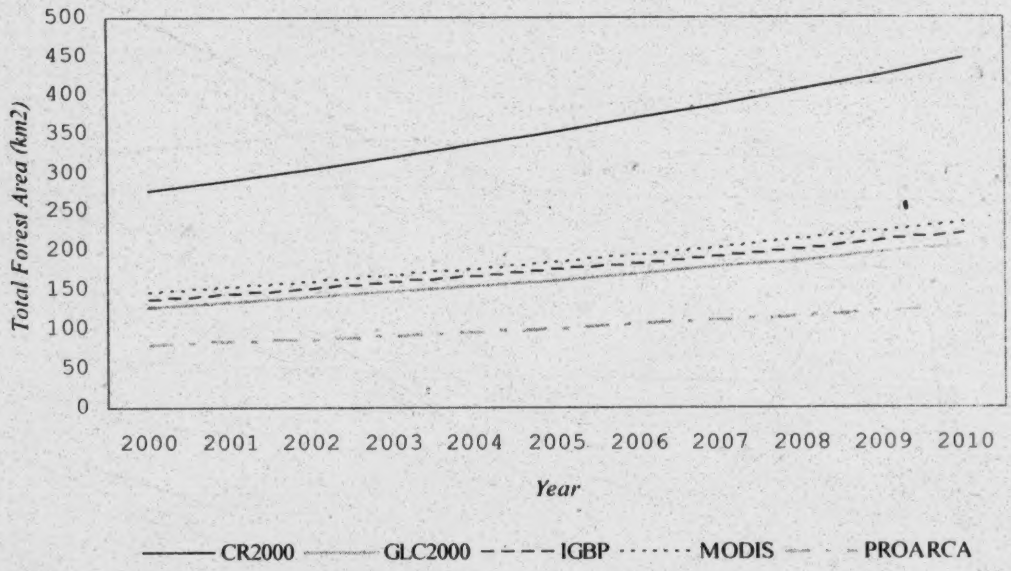

Figure 2.2 Ten-year forecasted total forest area (km2) assuming a constant +4.91km2/yr rate of change.

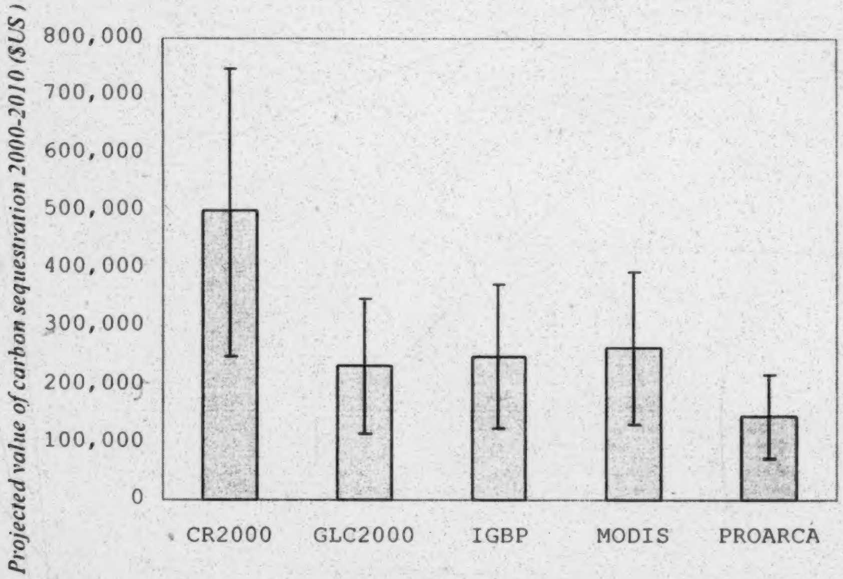

Figure 2.3 Projected value (2000-2010) of carbon sequestration from the CR2000 and the four land cover maps for the Santa Rosa study site.

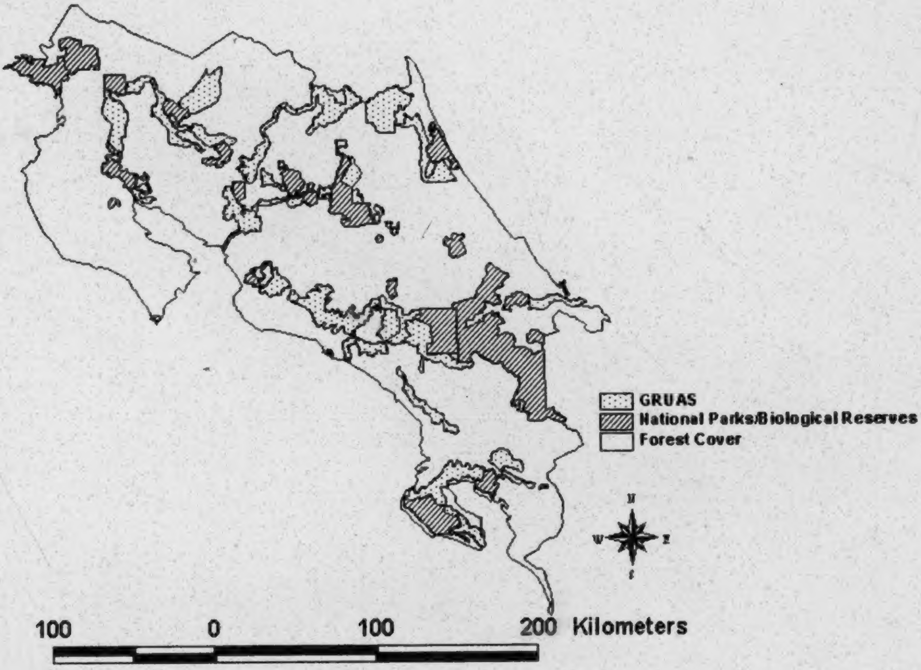
GRUAS
National Parks/Biological Reserves
Forest Cover
N
W
E
S
100
0
100
200 Kilometers

Figure 2.4 Areas of national parks, biological reserves and the predicted locations of the GRUAS corridors superimposed over the CR2000 forest cover data.

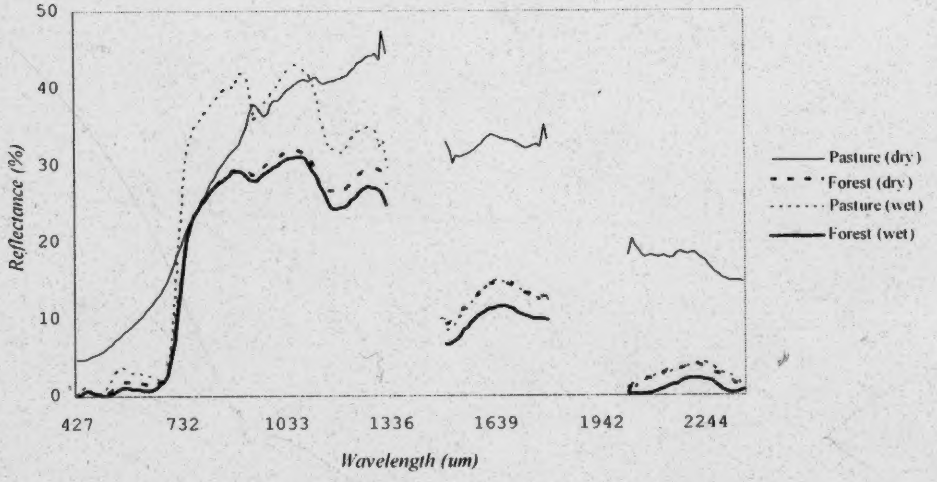

Figure 2.5 Spectra of pasture and forest in the dry and wet seasons as observed by the Hyperion hyperspectral satellite sensor for Santa Rosa.

Chapter 3: Calibration and assessment of seasonal changes in leaf area index of a tropical dry forest in different stages of succession[1]

3-1. Introduction

Tropical forests comprise approximately 47% of the global forest cover (FAO 2001) and seasonally dry tropical forests (T-df) comprise 42% of tropical forests. Ecologically, abiotic (e.g., water and biotic (e.g., competition) stresses are among the lowest in the T-df and tropical moist forests (Ewel 1999). Consequently, the T-df and tropical moist forest life zones have been the preferred ecosystems for human settlement and agricultural and animal husbandry practices (Piperno and Persall 2000).

According to the Holdridge life zone system, tropical dry forests are located in areas that have a biotemperature greater than 17ºC and 500 - 2000 mm of precipitation a year and a potential evapotranspiration ratio of 1-2 (ratio of the mean potential evapotranspiration to mean annual precipitation – a measure of humidity) (Holdridge 1967). In addition, T-dfs have an extended dry season with 4-6 months of little or no precipitation (Holdridge 1967, Janzen 1983, Lüttge 1997). In general, the T-df is a mix of deciduous (with variable timing of leaf fall) and evergreen species. Although many of the woody species in the T-df are drought deciduous (Frankie et al. 1974, Bullock and Solís-Magallanes 1990, Lobo et al. 2003), the number of species or individuals with this phenological response varies both with successional stage (stage of regeneration) and topography.

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[1] A version of this chapter has been published as Kalacska M., Calvo-Alvarado J.C. Sanchez-Azofeifa G.A. "Calibration and assessment of seasonal changes in leaf area index of a tropical dry forest" Tree Physiology 25:733-744. 2005. Reprinted with permission from Heron Publishing.

In woody species, leaf area is the exchange surface between the photosynthetically active component of the vegetation and the atmosphere, (Turner et al. 1999, Cohen et al. 2003, Fernandes et al. 2003, Fournier et al. 2003) and controls the light, thermal and hydric conditions within the canopy (Fournier et al. 2003). A simple measure of the amount of foliage is the leaf area index (LAI), the one-sided foliage area per unit ground area (projected one sided LAI; Fournier et al. 2003) which is unitless. LAI is often estimated by direct methods, such as destructive sampling, litter traps and allometric methods (Gower et al. 1999) or by optical methods such as gap fraction analysis (Chen et al. 1997). See Ross 1981, Welles 1990, Welles and Cohen 1996 and Fournier et al. 2003 for a comprehensive review. Destructive sampling and litter traps are labor intensive (Dufrène and Bréda 1995, Maass et al. 1995, Leblanc and Chen 2001) and allometric relationships are subject to many uncertainties (Chen et al. 1997). Therefore, optical methods are often preferred because LAI estimates can be completed relatively rapidly and accurately (Dufrène and Bréda 1995, Leblanc and Chen 2001). Once LAI values surpass 6.0 (Gower et al. 1999) however, optical techniques tend to saturate and destructive techniques may be more reliable (Leblanc and Chen 2001) although more expensive.

Plant-area index can be estimated with several optical instruments (e.g. LAI- 2000 (LI-COR, Lincoln NE), Sunfleck Ceptometer (Decagon Devices, Pullman WA). The LAI-2000 Plant Canopy Analyzer estimates the amount of radiation that infiltrates the canopy. The instrument is composed of five concentric silicon rings with fields of view centred between 7° and 68° (average

35°) and it measures diffuse sky radiation (<490nm to minimize scattering effects) through a hemispherical lens (LI-COR 1992). Although true LAI is solely a measure of foliage, tree trunks, branches, etc. also intercept incoming light and contribute to the measurements taken with optical instruments such as the LAI-2000 (Kucharik et al. 1998). In general, these instruments cannot discriminate between foliar and the woody components of the canopy.

Data on LAI from the tropics is sparse when compared with temperate and boreal environments. In the entire global LAI database, only 8% of the studies are from tropical regions (Asner et al. 2003) and temporal LAI studies from T-dfs are even scarcer. Yet quantification of temporal changes in LAI in T-dfs is important for understanding tropical ecosystem processes (Maass et al. 1995). Techniques for calibrating optical estimates differ according to canopy type (i.e. needle, broadleaf, mixed). With some exceptions, few studies have investigated the relationship between LAI determined by semi-direct techniques, such as litter traps, and optical estimates of LAI (e.g. Chason et al. 1991, Fassnacht et al. 1994, Dufrène and Bréda 1995 and Maass et al. 1995, Cutini et al. 1998).

The main objective of our study was to calibrate optical estimates of LAI from the LAI-2000 based on LAI derived from leaf litter data. We developed a robust method for determining LAI from leaf litter data in a tropical dry forest environment. As an application of the results, seasonal variations in LAI for the three successional stages in a T-df located in Costa Rica are presented.

3-2 Methods

3-2.1. Study Area

The study area, located in the Santa Rosa sector of the Área de Conservación Guanacaste (ACG) in Northwest Costa Rica (10° 48' 53"N, 85° 36' 54"W; Janzen 2000, Allen 2001) consists of secondary forest in various stages of regeneration with different land-use histories (Janzen 1986, 1988*a-c*, 2000, Kalacska et al. 2004). We refer to three different stages of succession in Santa Rosa: early, intermediate and late (Table 3.1). Total above ground biomass for the region is154.8 Mg ha^{-1} (± 13.05) based on a year 2000-2001 census (J.A. Tosi Jr. et al. Tropical Science Center, San José, Costa Rica unpublished). The climate in the region is characterized by six months with little or no precipitation and a total highly variable yearly precipitation (915-2558mm; Janzen 1993). The soils are young volcanic soils with high clay content (Gerhardt and Fredriksson 1995). They are brownish with moderate to shallow depths and are well to excessively well drained (Tropepts) (Vásquez Morera 1983)

3-2.2. Optical Leaf Area Index

Foliar LAI (L_f) can be calculated as (Leblanc and Chen 2001):

$$L_f = L_t(1-\alpha) = \frac{L_e(1-\alpha)}{\Omega} \qquad (1)$$

where α is the ratio of woody area (WAI) to total element area (plant area index -PAI) and L_t is LAI estimated by the instrument (PAI). The term Ω refers to a clumping index of the foliage at all scales (Leblanc and Chen 2001, Fournier et al. 2003) and L_e is the effective leaf area index: instrument LAI (L_t) with the contribution of the woody material (WAI) removed. We acknowledge that that branch geometry and architecture is as important as foliage in determining the light interception by the canopy (Chen and Black 1992, Kucharik et al. 1998). And that if such clumping at the crown level is significant optical estimates of LAI may be underestimated (Fournier et al. 2003). In addition, it has also been estimated that without any degree of leaf grouping, a tree would not be able to sustain an LAI greater than 6.0 because of self shading (Russell et al. 1989). However, due to the number of species with varying branch geometries (up to >100 woody species per ha representing >40 families in the intermediate stage) and no one dominant species (Kalacska et al. 2004) for the purposes of this paper we did not consider leaf aggregation in our estimations of LAI (i.e. $\Omega = 1$). In addition, because it has been shown that certain species found in our study area (e.g. *Gliricidia sepium*) do not have significant leaf clumping (Harrington and Fownes 1995) we believe for the purpose of this study it is acceptable to conduct these analyses with our estimates of LAI.

Leaf Area Index was estimated with the LAI- 2000 Plant Canopy Analyzer on eight occasions from December 2001 to April 2003 in sixteen 30 x 60m plots of different successional stages (7 early, 6 intermediate and 3 late). Arroyo-Mora (2002) found that 40% of the forest is intermediate, 27% is late, 19% is early and 12% is pastureland (i.e. very early regeneration). Therefore, the number of plots for each stage was chosen to be proportional to the area each stage covers in the study area while also taking into account differences in heterogeneity in the canopy layer (i.e. the canopy in the late stage is more homogeneous compared to the early or intermediate stages) (Arroyo-Mora et al. 2005). The measurements were made using an offset-grid sampling scheme where the maximum surface area of the plots was covered without overlap of the measurements (Figure 3.1).

In each early successional plot we took 100 measurements, each a roughly triangular area of 5 x 6m covering 83% of the total plot area. In each intermediate successional plot we took 36 measurements, each roughly a triangular area of 8 x 10m covering 80% of the total plot area. And in each late successional plot we took 12 measurements, covering an area of 15 x 18m encompassing 90% of the total plot area. We took reference (above canopy radiation) measurements both before and after each site. In addition, the sensor was fitted with a 45° view cap to eliminate the image of the operator from the field of view and be consistent with the sampling scheme. All measurements were taken under as uniform sky conditions as possible.

In addition, to assess the contribution of the woody component of the canopy, during the final data collection in March 2003 we took hemispherical photographs (Nikon CoolPix995) in each of the sites. We took ten photographs in each stage. These photographs were used to calculate WAI using Gap Light Analyzer v. 2.0 (SFU – IES 1999). This program extracts information on forest canopy structure (gap fraction, canopy openness, effective LAI) from true-color hemispherical photographs (SFU – IES 1999).

3-2.3. Leaf Litter

In September 2002 (peak of rainy season), ninety 0.5 x 0.5m standard mesh leaf litter traps were placed in three of the plots (30 traps - total surface area of 7.5m^2 per plot) where LAI-2000 measurements were being taken (1 early, 1 intermediate and 1 late). In each site, the traps were placed in ten offset rows of three to maximize the area covered. Leaf litter was collected at monthly intervals until the sites were leafless (end of the dry season, April 2003) for a total of five collections. In the late stage not all the trees lost their entire foliage, but the leaf cover was at its minimum during the final collection. From each trap, the litter was sorted by species and subsequently dried to constant weight using an air forced fan oven at 80°C. Prior calibration showed that 2.5 hrs were necessary to reach constant weight for all samples. The weight was recorded for each species separately. All unidentifiable remains were grouped into one category and weighed separately from the known species.

3-2.4. Specific leaf area

In August 2003, 15 fresh leaves were collected from all vegetation with a DBH greater or equal to 5cm in the three plots where the litter traps had been located. The area of the leaves was measured with the LI-COR 3000A portable leaf area meter before they were dried to constant weight (at 80°C). Subsequently, the leaves were weighed and specific leaf area (SLA) values were calculated for each species (Appendix 3.1). For the unknown category and those species for which we did not have SLA values we used a general leaf weight/leaf

area relationship calculated from the sixty-three species listed in Appendix 3.1:
area(m^2) = 0.0119 x weight(g)+0.0028 (R^2=0.86, P<0.001).

In this study, we will refer to raw estimates of LAI from the LAI-2000 (L_t from Eqn. 1) as Plant Area Index (PAI). Once the contribution of WAI has been removed from the PAI we refer to those values as LAIe (effective leaf area index, L_e from Eqn. 1). And finally, the LAIe values that have been calibrated with the leaf area from the litter traps are referred to as LAI (L_f from Eqn. 1).

3-2.5. LAI-2000 calibration

For the calibration of the LAI-2000 estimates we first calculated total leaf area for the leaves of each species from the unique SLA values. Leaf area was then converted to LAI by dividing by the area covered by the traps (i.e. 7.5m^2). LAI for the first time period (September) is the sum of the LAI values from each collection. For each subsequent time period, the total LAI from the previous collection is subtracted. With LAI values for each collection, we examined the relationship between the LAI-2000 estimates and the litter traps through least-squares linear regression. The resultant regression models as described in the subsequent sections serve as the calibration models for the LAI-2000 estimates.

3-2.6. Additional Analyses

To test the precision of the number of species captured, leaf weight and leaf area from the litter traps we conducted a series of graphical and empirical tests as described below. By solving for Δ in Eqn. 2 (Steidl and Tomas 2001), we calculated the minimum detectable difference in weight of leaf litter collected in the different stages.

$$n = \frac{2\sigma^2\left(Z_{\frac{\alpha}{2}} + Z_\beta\right)^2}{\Delta^2} \qquad (2)$$

where n is the number of traps, σ is the pooled standard deviation and 1-β the power level to detect a minimum biologically important difference (Δ) (Steidl and Tomas 2001). In our analysis, $\alpha = \beta = 0.1$ and therefore, $Z_{\alpha/2} = 1.64$ and $Z_\beta = 1.28$ (from statistical table).

The precision of the leaf weight and subsequent leaf area for each collection in each stage was calculated with Eqn. 3 (Steele et al. 1997).

$$AE\% = \sqrt{\frac{n}{(t_\alpha^2 CV^2)}} \qquad (3)$$

where AE is the actual error, n is the number of traps, CV is the coefficient of variation (in percent) and $t_\alpha = t_{0.05}$.

3-3. Results

3-3.1 Leaf litter traps

We collected the greatest amount of leaf litter from the intermediate stage (3559.1g) followed by the late (2950.0g) and the early (2252.9g) stages (Table 3.2). The "leaves" category is composed of all the identifiable species. The "unknown" category is composed of leaf matter unidentifiable to species and the "other" category is composed of twigs and other non-leaf material (excluding fruits and seeds). Of the total amount of litter, the intermediate stage has the greatest proportion of leaf matter not identifiable to species (29%) followed by the early (19%) and the late (16%). We found that there is a significant difference in total mean leaf fall per trap for the three stages (Kruskal Wallis Rank Test: F = 4.36, P = 0.039). In addition, pair-wise tests found differences in total mean leaf fall between the early and intermediate stages (Welch-Modified two sided t-test: t = -6.50, P < 0.001), the intermediate and late stages (t = 4.62, P < 0.001) and the early and late stages (t = -3.22, P = 0.002).

A breakdown of the leaf component of the litter is shown in Figure 3.2. The intermediate stage has the greatest percentage of lianas per sample with the exception of the fourth collection where the late stage contains the greatest percentage of lianas. In general, the percentage of unknown leaves decreases with each collection. Figure 3.3 illustrates the percentage of leaf area lost during each collection. In the early and late stages the majority of the foliage is lost in February whereas in the intermediate stage the majority of the foliage is lost in March before the final collection. In the early and intermediate stages there is a small second peak of leaf area lost in November composed of leaves of both trees and lianas. For the late stage the leaf area lost increases with each collection to its maximum in February and then decreases for the final collection in March. In addition, the fourth collection (February – windiest month in the study area) had the greatest number of species for each stage (54, 56 and 41 species respectively).

The greatest precision in both leaf litter weight and area is when the data from the five collections are pooled and the effects of leaf phenology are removed. By following the method described by Finotti et al. (2003) to determine the optimal sampling size for litter trap studies, it was found that the overall mean weight of leaf litter per trap (accuracy) generally stabilized after 10 traps (500 bootstrap replications (sampling with replacement by iteratively drawing from the original data – verifies replicability)). Similar to the results from Finotti et al (2003), the accuracy in the mean did not improve much with more than 10 traps. Contrarily to Finotti et al. (2003) however, the coefficient of variation (precision of the mean) did not stabilize after any number of traps because of the variability in litter weight per trap. For determining the accuracy of the mean litter weight per trap, thirty traps was excessive, however, ten traps (optimal for accuracy) are not sufficient for estimating the precision of the mean.

With thirty traps, the result of leaf weight and area are acceptable (in terms of uncertainty – Tables 3.3 and 3.4) in overall estimates disregarding the different seasons. The late stage provided the best estimate (8% and 12% uncertainty in weight and area respectively) because the canopy is more uniform than the other stages. Nevertheless, this approach to estimate LAI during the transition from the wet to the dry season is less precise (Table 3.3) due to the variable timing of leaf fall for the different species as well as the non uniform spatial distribution of trees and species, both of which increase variability.

The cumulative number of species per cumulative number of traps (1-30), based on 500 randomizations without replacement is illustrated in Figure 3.4. For all three stages the number of species captured per cumulative number of traps (species observed) is illustrated in Figure 3.4. For the three stages half the total number of species was reached with 4, 3 and 4 traps respectively. Because the number of species sampled from a community is an underestimation of the true number of species (Chazdon et al. 1998) we examined a number of species richness estimators described in Colwell and Coddington (1994) and Chazdon et al. (1998). We found that for our data, the Incidence-based Coverage Estimator (ICE) performed the best. It is an indicator that is based on species found in 10 or fewer sampling units (Lee and Chao 1994, Chazdon et al. 1998, Colwell 2002). ICE stabilized after 21 traps for the late stage and 20 traps for the early stage (Figure 3.4). None of the indices were stable for the intermediate stage. The asymptotic shape however, of the actual number of species captured curve for the intermediate stage indicates that 30 traps were sufficient. One possible explanation for the failure of the indicators to reach a stable value for the intermediate stage is that there are numerous species that only appeared in one trap each. This indicates a more patchy or heterogeneous distribution of the species and thus affects the results from the estimators.

The mean, standard error and standard deviation of SLA for the species in Appendix 3.1 are 237.6 cm^2g^{-1}, 15.0 cm^2g^{-1} and 117.6cm^2g^{-1} (500 bootstrap replications) respectively. The range of SLA values is 70.5 cm^2g^{-1} (*Roupala Montana*)- 634.7 cm^2g^{-1} (*Sciadodendron excelsum*). Based on a jackknife estimate of the mean (identifies outliers), the two species with the greatest influence on the mean SLA are *Sciadodendron excelsum* (634.7 cm^2g^{-1}) and *Maclura tinctora* (456.8 cm^2g^{-1}).

Because sorting the leaf litter by species is both difficult and time consuming we compared the sorted leaf area values to unsorted data. In addition, in certain studies (Maass et al. 1995) authors have used unsorted SLA to estimate

LAI from litter traps. Because of the large standard deviation in all results of mean SLA (500 replicates without replacement of a random sample of 5 – 63 species), there is no statistical difference in the mean SLA with any number of species from 5 to 63. Figure 3.5 however, illustrates the different LAI values obtained from average SLA values (10 – 60 species) and the actual LAI obtained if the litter is sorted by species and unique SLA values are used for each species. There is a gross overestimation of LAI in all stages if the litter is not sorted by species, especially when the weight of the leaf litter is above 400g such as for the last two collections (Figure 3.5).

3-3.2 LI-COR 2000 calibration

The values of PAI from the LAI-2000 and the values for LAI from the traps for each collection are listed in Table 3.5 for the three stages. WAI calculated from hemispherical photographs was 0.40±0.14 for the late stage, 0.40±0.27 for the early stage and 1.07±0.43 for the intermediate stage. From Eqn. 3, we obtained a range of uncertainty of the mean LAI-2000 estimates of 7.3 – 12% for the early stage, 10 – 15.9% for the intermediate and 8.7 – 16.1% for the late stage. Yet, there was one late plot in the February 2003 collection that had an unusually high uncertainty (31.6%). We believe this was because there was a range of canopy conditions where, while the majority of the canopy was not completely leafless, there were patches that were and therefore, the coefficient of variation was relatively high (57%) in comparison to the other plots. The contribution of the WAI and the subsequent contribution of the foliage to the PAI estimation from the LAI-2000 are also listed in Table 3.5. LAIe is the value of leaf area estimated by the LAI-2000 after the WAI contribution is removed. There is one LAI-2000 reading missing from Table 3.5 (early intermediate and late stages). During those two data collections, the instrument malfunctioned due to low batteries and the data were lost before they could be transferred to a computer from the data logger. In all collections except when the trees are leafless, the LAI-2000 underestimates leaf area index by 16.5% (intermediate stage – February) to 60% (intermediate stage – January). In each stage however, the LAI-2000 overestimates "leaf area index" when the trees are leafless due to the contribution of the WAI.

The best relationship between LAI values from the litter traps (y) and LAIe from the LAI-2000 (x) is in the late stage ($y= 3.42x-4.58$, $R^2=0.92$, $F=45.19$, $P<0.05$, 5 points in time) followed by the early ($y=1.84x-1.08$, $R^2=0.82$, $F=13.71$, $P<0.05$, 6 points in time) and intermediate stages ($y = 1.79x-0.698$, $R^2=0.76$, $F=9.66$, $P=0.05$, 5 points in time). With all the sample points from the three stages combined the relationship becomes: $y=2.12x-1.55$ ($R^2=0.78$, $F=49.75$, $P<0.05$, 16 points in time).

3-3.3. Seasonal LAI

By using the relationships illustrated above, LAIe was converted to LAI for each of the eight LAI-2000 data collections. Seasonal variation in LAI for the three stages is illustrated in Figure 3.6. The data were fitted to a third order polynomial to graphically illustrate the seasonality of LAI. Solving for the derivative of the polynomial functions gave the months where LAI was at its minimum and maximum. The three stages yielded different results (Figure 3.6):

effects of the wind until February when soil moisture is very low and the canopy becomes more open to the wind. Once the canopy loses approximately 30 % of the total leaf biomass, the lianas begin to lose their leaves. But, because of the drought and wind the majority of the lianas (in the late stage) lose the greatest proportion of their leaf biomass during the driest time of the year rather than in lesser proportions at a more constant rate throughout the transition from rainy to the climax of the dry season. Contrary to past research, Andrade et al. (in press) illustrate in a study from Panama that as the dry season progresses, lianas tap in to progressively deeper water sources. A pattern they did not observe in large trees. Lianas have also been shown to have deeper root systems than the surrounding trees (Jackson et al. 1995). In addition, Andrade et al. (in press) suggest that the architecture of the lianas enhances their stem water storage capability relative to their leaf transpiration area. This all could be part of a plausible explanation for the leaf retention pattern observed in the leaf litter data.

The late stage is the most uniform in canopy architecture. The early and the intermediate stages are very heterogeneous in comparison; the early stage because of the numerous gaps and the intermediate stage because of the increased woody matter from the lianas. This heterogeneity is partially responsible for the relationships between the LAI-2000 and trap LAI estimates in the early and intermediate stages not being as strong.

The composition of the litter traps in this study (i.e. foliage being predominant) (Table 3.2) is similar to the result from numerous other studies (Muoghalu et al. 1993, Morellato 1992, Scott et al. 1992, Haase 1999, Sundarapandian and Swamy 1999). The total litter fall in this study (3.0 – 4.75 Mg ha^{-1}yr^{-1}) is consistent with values reported in other T-dfs but lower than values reported for wetter forests (Table 3.6).

The variation in litter fall observed is expected because differences in species composition, successional stage and microclimate will greatly affect litter fall patterns (Sundarapandian and Swamy 1999). While the majority of studies report a significant peak in leaf fall during the dry season, in certain areas a smaller peak in litter fall has been noted at the end of the wet season (Proctor et al. 1983, Muoghalu et al. 1993). This was attributed to wind, heavy rain and periodicity of leaf fall following environmental parameters. In this study a similar small second peak is seen at the end of the wet season for the early and intermediate stages (Figure 3.3). This peak in the wet season may also be related to a short period of water stress during the wet season. While there are more species represented in the December collection for both stages compared to the November collection, there is a greater amount of leaves but fewer species collected in November.

The leaf fall pattern in the intermediate stage differs temporally from the early and late stages (Figure 3.3). In the early stage the canopy is open and thus exposed to the wind. In addition, with root systems that are shallower the trees in the early stage compared to the semi-evergreen species of the late stage experience a more rapid loss of soil moisture than the other stages (Sobrado 1991). The majority of the vegetation in the early stage is from the pioneer guild with the appearance of species from the intermediate guild. As a result, the majority of the foliage is lost earlier in the transition season. In the late stage there is a mix of vegetation from both the intermediate and shade tolerant guilds. There was less disparity in the amount of foliage collected by the individual traps in this stage indicating a more homogenous canopy. In the intermediate stage the percent of the foliage lost increased with each collection. A multitude of factors have been found by other studies to account for the timing and degree of deciduousness as discussed above. The variability expressed by the different stages is expected (Bullock and Solís-Magallanes 1990) because of differences in species composition and microclimate.

The uncertainty in the estimation of weight and area is higher for the early and intermediate stages than the late in the transition season. One way to reduce the uncertainty is to increase sampling effort by increasing the number of traps or increasing the size of the traps to 1m x 1m. Both are very time consuming however, and it is doubtful that the increase in time and effort will reduce the uncertainty significantly. We consider this study to contribute to the understanding of this sampling issue and hence the results may fuel further studies which will improve upon this methodology. Nevertheless, we consider the results acceptable for our objectives and useful for understanding the seasonal variation of LAI in three stages of T-df regeneration.

SLA has been used extensively to calculate total leaf area from litter traps (Neumann et al. 1989, Chason et al. 1991, Maass et al. 1995, Bouriaud et al. 2003). Very few studies however, have documented the relationship between leaf area index from SLA, leaf litter and optical estimates of LAI. In the studies where such a relationship is reported, unless the study site is dominated by a single species (e.g. Bouriaud et al. 2003), SLA is an average of many species (e.g. Maass et al. 1995). In Figure 3.5 we compare the results of sorting SLA by species and then calculating a leaf area index versus an average SLA for multiple species. We found that in an environment with a large range of SLA values such as our study site, it is imperative to calculate SLA for as many species as possible. The values for leaf area were greatly exaggerated when aggregate SLA values were used, regardless of how many species were averaged (Figure 3.5).

Once the WAI was removed from the LAI-2000 readings, the optical LAIe estimates had a strong relationship with the leaf area index derived from the litter traps. In a similar study, Maass et al. (1995) report an overall relationship of y = 1.03x+0.87 (R^2 = 0.95) where y is optical LAI (from a Sunfleck Ceptometer), and x is litter trap LAI. If we reverse the overall relationship to have the same x and y as Maass et al. (1995), our optical – litter LAI relationship becomes: y = 0.37x+1.09 (R^2=0.78, P<0.001). According to Maass et al. (1995) the greater LAI values from the optical estimates are due to leaf retention from a few deciduous species beyond the end of the litterfall collection and the presence of some evergreen species. It is unclear however, whether the contributions of woody elements (i.e. branches) were removed from their optical LAI estimates.

In this study, the amount by which the LAI-2000 underestimates LAI compared to litter traps is consistent with values from other ecosystems (Chason et al. 1991, Chen and Black 1991, Durfrène and Bréda 1995). These studies were conducted in mixed Oak and Hickory, Douglas Fir, Sessile Oak, European Beech and Sweet Chesnut stands. There are two readings however, where the percent difference between the LAIe and the litter traps is greater than 50% (Table 3.5).

An asynchronous leaf phenological cycle is apparent for the three stages (Figure 3.6). The difference in phase is most pronounced for the intermediate stage. This is supported by an analysis of the first derivative of the leaf phenology curve (Figure 3.6) that indicates a longer phenological cycle. During different months of the year, it is indistinguishable from either the early or the late stage. This asynchronicity could have important implications at a regional level if LAI is being extracted from remotely sensed data. Season of image acquisition is always a concern in the T-df, and depending on the goals of the study, the accuracy of derived LAI values may differ with respect to time. This study illustrates the need for a multi-temporal image analysis because examination of LAI – remotely sensed data relationships for a single time frame could lead to confusion especially from imagery acquired in the transition seasons. With respect to biogeochemical models that require LAI as an input (e.g. FOREST-BGC) (Running and Coughan 1988) these differences in phase in the seasonal LAI show the importance of examining a forest cover segregated by successional stage rather than a single input value even though the dependency of these models on accurate estimates of LAI decreases after a value of 3.0 (Waring and Running 1998). Studies regarding litter turnover do in many cases require SLA and this study will provide a general range that can be found for the T-df.

While calibration of optical LAI estimates is labor intensive we recommend that this calibration be used with caution in other T-df environments where the structure of the forest is different. At the very least, WAI needs to be established for each location after which either the specific relationships for the stages or the overall relationship may be used as a general calibration. If data regarding successional stages are available then the individual relationships would be more reliable.

The rationale for the calibration in this study is that LAI greatly affects the energy reflected to space and air-borne remote sensing instruments. Remote sensing is a relatively cost effective method of extracting information over large areas of the Earth's surface. The accuracy of remotely sensed products such as global land cover classifications (e.g. IGBP land cover data base, CCRS North and Central American Land Cover classification, MODIS land cover classification) however, is influenced by the ability to interpret the spectral signature of the various land covers some of which are dependent on LAI. Therefore, with solid relationships between remotely sensed reflectance and LAI, data on the extent and status of T-dfs in different stages of growth can be generated. Satellite image derived products such as estimations of fPAR are also increasing in popularity because it has been found such variables have a strong relationship to vegetation indices (e.g. vegetation greenness indices from MODIS) (Waring and Running 1998). In addition to contributing to the general understanding about T-dfs, this data and products derived from it are also important for developing conservation policies and payments for environmental services (Daily et al. 1997, Chomitz et al. 1998).

3-5. References

Allen W. 2001. Green Phoenix, Restoring the Tropical Forets of Guanacaste, Costa Rica. Oxford: Oxford University Press. pp. 310.

Andrade J.L., Meinzer F.C., Goldstein G. & Schnitzer S.A. in press Water uptake and transport in lianas and co-ocurring trees of a seasonally dry tropical forest. Trees: Structure and Function.

Arroyo-Mora J.P. 2002 Forest cover assessment, fragmentation analysis and secondary forest detection for the Chorotega Region, Costa Rica. University of Alberta. pp. 111.

Arroyo-Mora J.P., Sanchez-Azofeifa G.A., Rivard B., Calvo-Alvarado J.C., Kalacska M., Janzen D.H. 2005. Secondary forest detection in a Neotropical dry forest: complementary use of IKONOS and Landsat 7 ETM+ imagery. Biotropica, Accepted.

Asner G.P., Scurlock J.M.O & Hicke J.A. 2003 Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. Global Ecol Biogeogr, 12: 191-205.

Bouriaud O., Soudani K. & Bréda N. 2003 Leaf area index from litter collection: impact of specific leaf area variability within a beech stand. Can J Remote Sens, 29: 371-380.

Bullock S.H. & Solis Magallanes J.A. 1990 Phenology of canopy trees of a tropical deciduous forest in Mexico. Biotropica, 22: 22-35.

Chason J.W., Baldocchi D.D. & Huston M.A. 1991 A comparison of direct and indirect methods for estimating forest canopy leaf area. Agr Forest Meteorol, 57: 107-128.

Chazdon R L., Colwell R.K., Denslow J.S. & Guariguata M.R. 1998 Statistical Methods of Estimating Species Richness of Woody Regeneration in Primary and Secondary Rain Forests of Northeastern Costa Rica. *In* Forest Biodiversity Research, Monitoring and Modeling (Eds. Dallmeier F. and Cominsky J.A.), UNESCO, Paris. pp. 285-309.

Chen J.M. & Balck T.A. 1991. Measuring leaf area index of plant canopies with branch architecture. Agr Forest Meteorol, 57:1-12.

Chen J.M, Rich P.M., Gower S.T., Norman J.M. & Plummer S. 1997 Leaf area index of boreal forests: theory, techniques and measurements. J Geophys Res, 102: 24429-24443.

Cohen W.B., Maiersperger T.K., Gower S.T & Turner D.P. 2003 An improved strategy for regression of biophysical variables and Landsat ETM+ data.

Remote Sens Environ, 84: 561-571.

Colwell R. K. 2002. EstimateS v.6.0b1 Statistical Estimation of Species Richness and Shared Species from Samples. http://viceroy.eeb.uconn.edu/estimates

Colwell R.K. & Coddington J.A. 1994 Estimating terrestrial biodiversity through extrapolation. Philos T Roy Soc B, 345: 101-118.

Cutini A., Matteucci G. & Scarascia Mugnozza G. 1998 Estimation of leaf area index with the Li-Cor 2000 in deciduous forests. Forest Ecol Manag, 105: 55-65.

Dufrêne E. & Bréda N. 1995 Estimation of deciduous LAI using direct and indirect methods. Oecologia, 104: 156-162.

Ewel J.J. 1999 Natural systems as models for the design of sustainable systems of land use. Agroforest Syst, 45: 1-21.

FAO 2001 COFO-2000/INFS-Global Forest Resources Assessment 2000. Food and Agriculture Organization of the United Nations, Rome.

Fassnacht K.S., Gower S.T., Norman J.M & McMurtrie R.E. 1994 A comparison of optical and direct methods for estimating foliage surface area index in forests. Agr Forest Meteorol, 71:183-207.

Fernandes R.F., Butson F., Leblanc S.G. & Latifovic R. 2003 Landsat-5 TM and Landsat 7 ETM+ based accuracy assessment of leaf area index products for Canada derived from SPOT-4 VEGETATION data. Can J Remote Sens, 29: 241-258.

Finotti R., Rodrigues Freitas S., Cerqueira R. & Vinicius Vieria M. 2003 A method to determine the minimum number of litter traps in litterfall studies. Biotropica, 35: 419-421.

Fournier R.A., Mailly D., Walter J.-M. & Soudani K. 2003 Indirect measurement of forest canopy structure from in situ optical sensors. *In* Methods for Remote Sensing of Forests: Concepts and Case Studies (Eds. Wulder M. and Franklin S.), Kluwer Academic Press. pp. 77-114.

Frankie G.W., Baker H.G. & Opler P.A. 1974 Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. J Ecol, 62: 881-919.

Gerhardt K. and Fredriksson D. 1995. Biomass allocation by broadleaf Mahogany seedlings, Swietenia macrophylla (King) in abandoned pastures and secondary dry forest in Guanacaste, Costa Rica. Biotropica, 27:174-182.

Gower S.T., Kucharik C.J. & Norman J.M. 1999 Direct and indirect estimation of leaf area index, FAPAR, and net primary production of terrestrial ecosystems. Remote Sens Environ, 70: 29-51.

Haase R. 1999 Litterfall and nutrient return in seasonally flooded and non-flooded forest of the Pantanal, Mato Grosso, Brazil. Forest Ecol Manag, 117: 129-147.

Holdridge 1967 Life Zone Ecology. Tropical Science Center, San Jose Costa Rica. pp.747.

Jackson P.C., Meinzer F.C., Bustamante M., Goldstein G., Franco A., Rundel P.W., Caldas L., Igler E. & Causin F. 1995 Partitioning of soil water among tree species in a Brazilian Cerrado ecosystem. Tree Physiol, 19: 717-724 .

Janzen D.H. 1983 Costa Rican Natural History. Chicago University Press, Chicago, pp. 816.

Janzen D.H. 1986 Tropical dry forests: the most endangered major tropical ecosystem. *In* Biodiversity (Wilson E.O.), National Academy Press, Washington. pp. 130-137.

Janzen D.H. 1988a Guanacaste National Park: Tropical ecological and biocultural restoration. *In* Rehabilitating damaged ecosystems (Cairns J.J.), CRC Press, Boca Raton, Florida. pp. 143-192.

Janzen D.H. 1988b Management of habitat fragments in a tropical dry forest: Growth. Ann Mo Bot Gard, 75: 105-116.

Janzen D.H. 1988c. Complexity is in the eye of the beholder. *In* Tropical rainforests: diversity and conservation (Almeda F. and Pringle C.M.), California Academy of Science and AAAS, San Francisco. pp. 29-51.

Janzen D.H. 1993 Caterpillar seasonality in a Costa Rican dry forest. *In* Caterpillars: Ecological and evolutionary constraints on foraging (Stamp N.E. and Casey T.M.), Chapman Hill, New York. pp. 448-477.

Janzen D.H. 2000 Costa Rica's Area de Conservacion Guanacaste: a long march to survival through non-damaging biodevelopment. Biodiversity, 1: 7-20 .

Kalacska M., Sanchez-Azofeifa G.A., Calvo-Alvarado J.C., Quesada M., Rivard B., Janzen D.H. 2004. Species composition, similarity and diversity in three successional stages of a seasonally dry tropical forest. Forest Ecol Manag 200: 227-247.

Kucharik C.J., Norman J.M. & Gower S.T. 1998 Measurements of branch area and adjusting leaf area index indirect measurements. Agr For Meteorol, 91: 69-88.

Leblanc S.G. & Chen J.M. 2001 A practical scheme for correcting multiple scattering effects on optical LAI measurements. Agr For Meteorol, 110: 125-139.

Lee S.M. & Chao A. 1994 Estimating population size via sample coverage for closed capture-recapture models. Biometrics, 50: 88-97.

Lobo J.A., Quesada M., Stoner K.E., Fuchs E.J., Herrerias-Diego Y., Rojas-Sandoval J. & Saborio-Rodriguez G. 2003 Factors affecting phenological patterns of Bombacaceous trees in seasonal forests in Costa Rica and Mexico. Am J Bot, 90: 1054-1063.

Lüttge U. 1997 Physiological Ecology of Tropical Plants. Springer-Verlag, Heidelberg, pp. 384.

Maass J.M, Vose J.M, Swank W.T. & Martinez-Yrizar A. 1995 Seasonal changes in leaf area index (LAI) in a tropical deciduous forest in west Mexico. Forest Ecol Manag, 74: 171-180.

Morellato L.P.C. 1992 Nutrient cycling in two Southeast Brazilian forests. I. Litterfall and litter standing crop. J Trop Ecol, 8: 205-215.

Muoghalu J.I., Akanni S.O. & Eretan O.O. 1993 Litterfall and nutrient dynamics in a Nigerian rain forest seven years after a ground fire. J Veg Sci, 4: 323-328.

Neumann H.H., Den Hartog G. & Shaw R.H. 1989 Leaf area measurements based on hemispheric photographs and leaf-litter collection in a deciduous forest during autumn leaf-fall. Agr Forest Meteorol, 45: 325-345.

Piperno D.R. & Persall D.M. 2000 Origins and Agriculture in the Neotropics. Academic Press. pp. 400.

Proctor J., Anderson J.M., Fogden S.C.L. & Vallack H.W. 1983 Ecological studies to four contrasting lowland rainforest in Gunung Mulu National Park, Sarawak. II. Litterfall, litter standing crop and preliminary observations on herbivory. J Ecol, 71: 261-283.

Ross J. 1981 The radiation regime and architecture of plant stands. Junk, London. pp. 418.

Running S.W. & Coughlan J.C. 1988 A general model of forest ecosystem processes for regional applications: I-Hydrologic balance, canopy gas exchange and primary production processes. Ecol Model, 42: 125-154.

Russell G., Jarvis P.G., Monteith J.L. 1989. Absorption of radiation by canopies and stand growth. In: Russell G., Marshall B. and Jarvis P.G. (Eds.) Plant Canopies: Their growth, form and function. Cambridge: Cambridge

University Press, pp 21-40.

Scott D.A., Proctor J. & Thompson J. 1992 Ecological studies on a lowland evergreen rainforest on Maraca Island, Roraima, Brazil. II. Litter and nutrient cycling. J Trop Ecol, 80: 705-717.

SFU-IES. 1999. Gap Light Analyzer V.2.0. Available online at: http://www.rem.sfu.ca/forestry/downloads/gap_light_analyzer.htm.

Sobrado M. 1991. Cost-benefit relationships in deciduous and evergreen leaves of tropical dry forest species. Funct Ecol, 5:608-616.

Steele R.D.G, Torrie J.H. & Dickey D.A. 1997 Principles and Procedures of Statistics: A Biometric Approach. WCB McGraw-HIll, Boston, pp. 666.

Steidl R.J. & Thomas L. 2001 Power Analysis and Experimental Design. *In* Design and Analysis of Ecological Experiments (Eds. Sheiner S.M. and Gurevitch J.), Oxford University Press, Oxford. pp. 14-36.

Sundarapandian SM. & Swamy P.S 1999 Litter production and leaf litter decomposition of selected tree species in tropical forests at Kodayar in the Western Ghats, India. Forest Ecol Manag, 123: 231-244.

Turner D.P., Cohen W.B., Kennedy R.E., Fassnacht K.S. & Briggs J.M. 1999 Relationships between leaf area index and Landsat TM spectral vegetation indices across three temperate zone sites. Remote Sens Env, 70: 52-68.

Vásquez Morera A. 1983. Soils In: Costa Rican Natural History, Janzen D.H. (Ed.) Chicago: University of Chicago Press. pp 63-65.

Waring R.H. and Running S.W. 1998 Forest Ecosystems: Analysis at Multiple Scales. Academic Press, Inc., San Diego, California. 370 pp.

Welles J.M. 1990 Some indirect methods of estimating canopy structure. Remote Sens Rev, 5: 31-43.

Welles J.M. & Cohen S. 1996 Canopy structure measurement by gap fraction analysis using commercial instrumentation. J Exp Bot, 47: 1335-1342.

Table 3.1 Description of the successional stages in the Santa Rosa sector of the ACG (200-300m elevation) adapted from Arroyo-Mora 2002 and Kalacska et al. 2004.

Stage	Canopy	Height (m)	Basal Area (m^2 ha^{-1})	Density (stems $0.1ha^{-1}$)	Species Density (Sp. $0.1ha^{-1}$)	Description
Early	1 stratum	7.5 ± 2.2	11.7 ± 5.4	112 ± 64	15 ± 7	-Predominantly deciduous trees. -Many shrubs, small trees with grasses and bare soil - Heterogeneous canopy.
Intermediate	2 strata	10.3 ± 3.4	30.1 ± 6.5	130 ± 35	29 ± 5	-Upper layer of canopy composed of fast growing deciduous species. -Lianas, and shade tolerant species form second layer. -Both deciduous and evergreen species.
Late	2 strata	15.0 ± 2.2	30.1 ± 6.5	107 ± 42	29 ± 7	-Shade tolerant species. -Little light reaches the canopy floor. -Evergreen species with overlapping tree crowns in upper canopy form continuous layer.

Table 3.2 Total composition of the leaf litter traps from the three successional stages: early, intermediate and late in Santa Rosa. Values in parentheses indicate percentage of total.

	Early	Intermediate	Late
Leaves	1,763g (67)	2,233g (50)	2,429g (73)
Fruits/seeds	104g (4)	275g (6)	60g (2)
Other	249g (10)	699g (15)	286g (9)
Unknown total	490g (19)	1,326g (29)	521g (16)

Table 3.3 Minimum detectable differences in weight (g) of leaf litter between the three successional stages: early (E), intermediate (I) and late (L) in Santa Rosa.

Collection	E – I	I – L	E – L
1	11	16	11
2	13	14	10
3	15	18	11
4	19	18	22
5	30	37	22
Overall	61	55	41

Table 3.4 Precision (% error) of the weight of leaf litter collected in the three successional stages (early, intermediate and late) in Santa Rosa and the precision (% error) of leaf area calculated from the leaf litter for the three stages.

Collection	Early area	Early weight	Intermediate area	Intermediate weight	Late area	Late weight
1	34	34	40	19	18	16
2	28	20	21	20	22	18
3	21	18	32	32	27	16
4	19	21	18	10	16	14
5	38	39	29	19	12	11
Overall	12	13	17	12	12	8

Table 3.5 Plant Area Index (PAI) from the LAI-2000 measurements, percent woody-area-index (WAI) where WAI = 0.40±0.27 for the early stage, 1.07±0.43 for the intermediate stage and 0.40±0.14 for the late stage, corresponding percent leaf contribution (%LAI), effective leaf area estimates from the LAI-2000 (LAIe), leaf area index from the litter traps (LAI-Trap) and percent underestimation of leaf area by the LAI-2000. All PAI and LAIe estimates have an uncertainty of ±0.11 which include errors in the measurements (0.1) and error propagation in the calculations (0.01).

Stage	Month	PAI	%WAI	%LAI	LAIe	LAI-Trap	% Diff.
Early	Sep	3.2±0.1	13	87	2.8±0.1	5.8±0.9	52
	Nov	3.5±0.1	11	89	3.1±0.1	5.4±0.8	42
	Dec	3.0±0.1	13	87	2.6±0.1	4.8±0.7	46
	Jan	3.1±0.1	13	87	2.7±0.1	4.1±0.5	34
	Feb	2.2±0.1	18	82	1.8±0.1	1.8±0.2	0.0
	Mar	1.9±0.1	22	78	1.4±0.1	0.0	Over
Intermediate	Sep	5.7±0.1	19	81	4.6±0.1	7.1±1.9	35
	Nov	-	-	-	-	6.2±1.5	-
	Dec	4.2±0.1	25	75	3.2±0.1	5.4±1.3	42
	Jan	2.9±0.1	37	63	1.9±0.1	4.7±1.1	60
	Feb	3.4±0.1	32	68	2.3±0.1	2.8±0.8	17
	Mar	2.2±0.1	48	52	1.2±0.1	0.0	Over
Late	Sep	2.9±0.1	14	86	2.5±0.1	4.0±1.5	38
	Nov	2.9±0.1	14	86	2.5±0.1	3.5±1.4	28
	Dec	2.8±0.1	14	86	2.4±0.1	2.9±1.2	18
	Jan	1.7±0.1	23	77	1.3±0.1	2.0±1.1	33
	Feb	1.8±0.1	23	77	1.4±0.1	0.8±0.7	over
	Mar	-	-	-	-	0.0	-

Table 3.6 Comparison of leaf litter production from various forest ecosystems

Location	Forest type	Leaf litter production	Source
Puerto Rico	Dry forest	2.5 Mg $ha^{-1}yr^{-1}$	Lugo et al. (1978)
Mexico	Dry forest	3.5 – 4.5 Mg $ha^{-1}yr^{-1}$	Maass et al. (1995)
Costa Rica	Dry forest	3.0 – 4.75 Mg $ha^{-1}yr^{-1}$	This study
India	Dry forest	5.76 – 8.65Mg $ha^{-1}yr^{-1}$	Sundarapandian and Swamy (1999)
Venezuela	Amazon Caatinga	4.95 Mg $ha^{-1}yr^{-1}$	Jordan 1985
Venezuela	Oxisol forest	5.87 Mg $ha^{-1}yr^{-1}$	Jordan 1985
Malaysia	Dipterocarp forest	6.3 Mg $ha^{-1}yr^{-1}$	Jordan 1985
Brazil	Seasonal flooded forest	7.53 – 10.27 t $ha^{-1}yr^{-1}$	Hasse (1999)
Panama	Moist forest	11.3 Mg $ha^{-1}yr^{-1}$	Jordan 1985
Ivory Coast	Evergreen forest	8.19 Mg $ha^{-1}yr^{-1}$	Jordan 1985
Puerto Rico	Rain forest	5.43 Mg $ha^{-1}yr^{-1}$	Jordan 1985
Costa Rica	Rain forest	7.83 – 12.4 Mg $ha^{-1}yr^{-1}$	Gessel et al. (1979), Parker (1994)
Australia	Rain forest	9.25 t $ha^{-1}yr^{-1}$	Brasell et al. (1980)

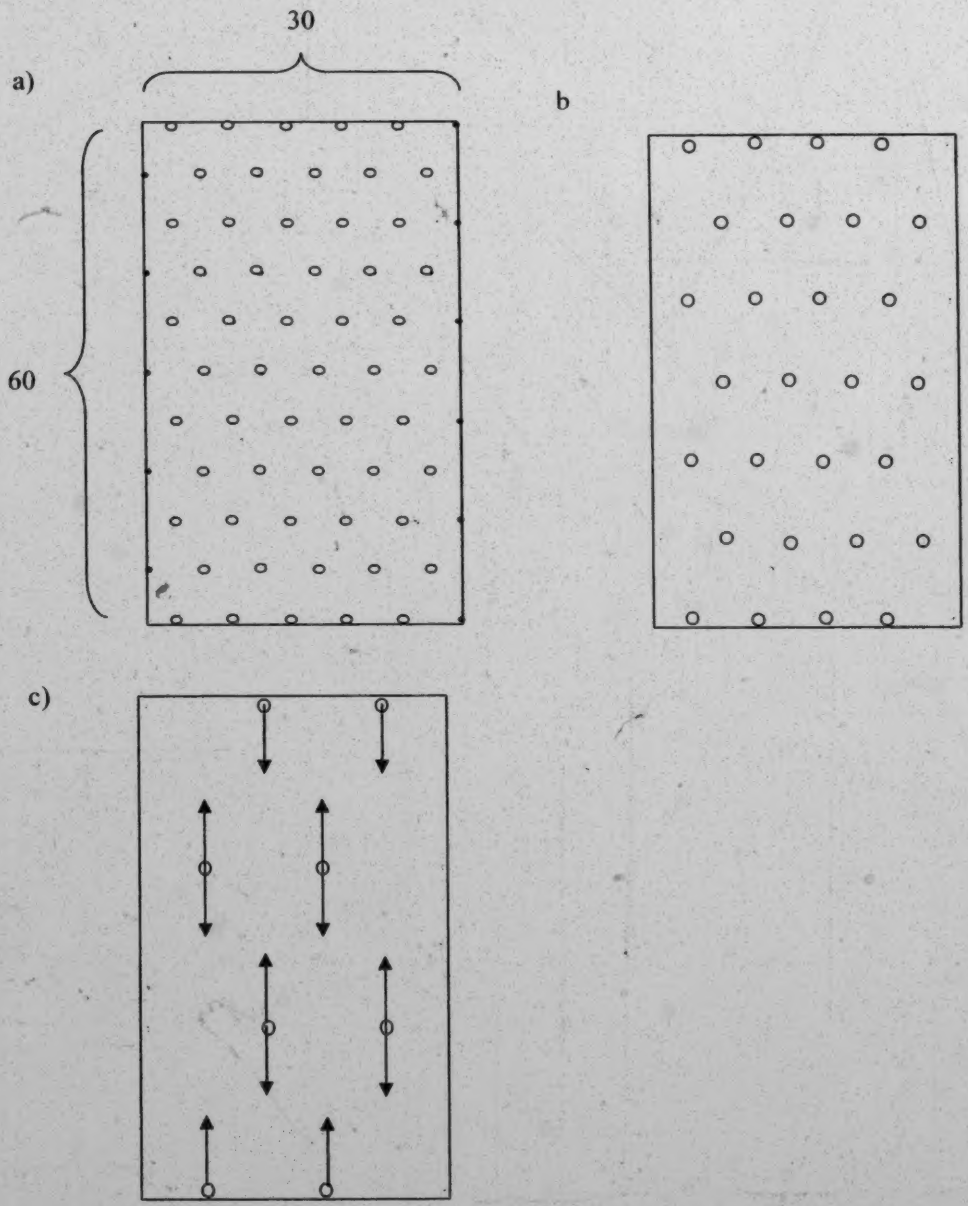
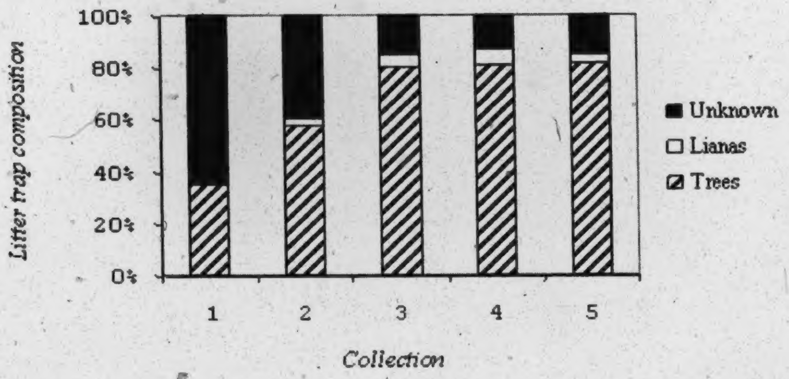
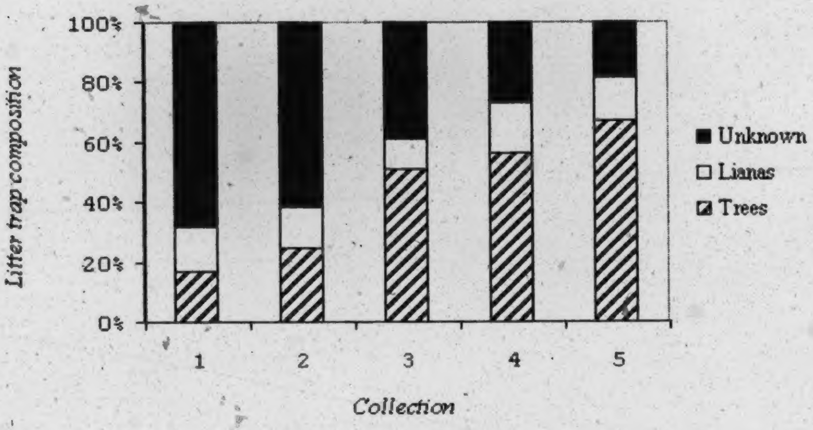


Figure 3.1. Example of LAI- 2000 sampling methodology. Estimates were taken at the apex of each triangle (white circle) in the direction of the long axis as illustrated by the arrows on the late stage plot diagram. a) early, b) intermediate, c) late

a)



b)



c)

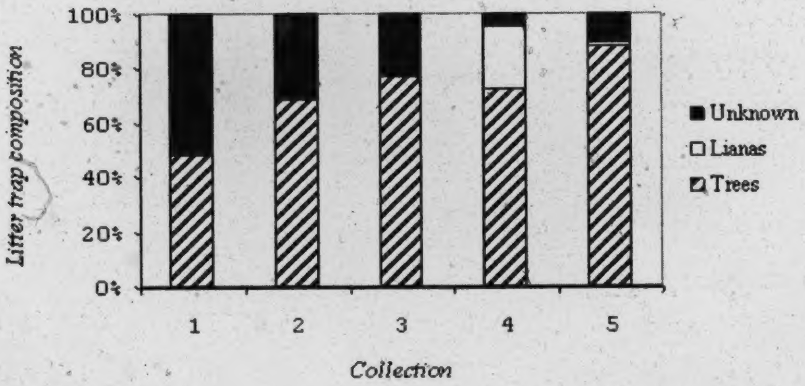


Figure 3.2. Leaf component of litter collected from the traps for the three stages in Santa Rosa sorted by trees, lianas and unknown a) early, b) intermediate and c) late.

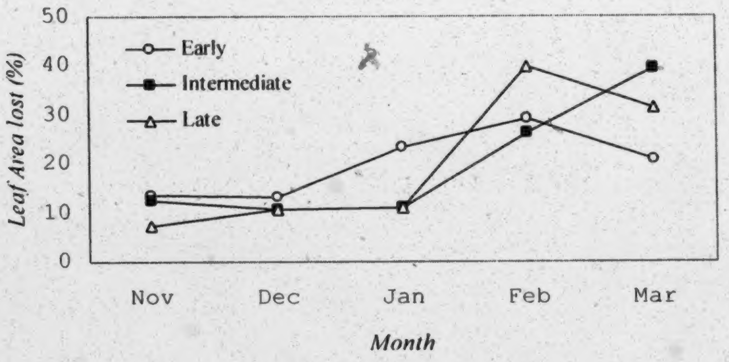


Figure 3.3 Percentage of the total leaf area lost by the canopy in the three stages (early, intermediate, late) per litter trap collection from September to March.

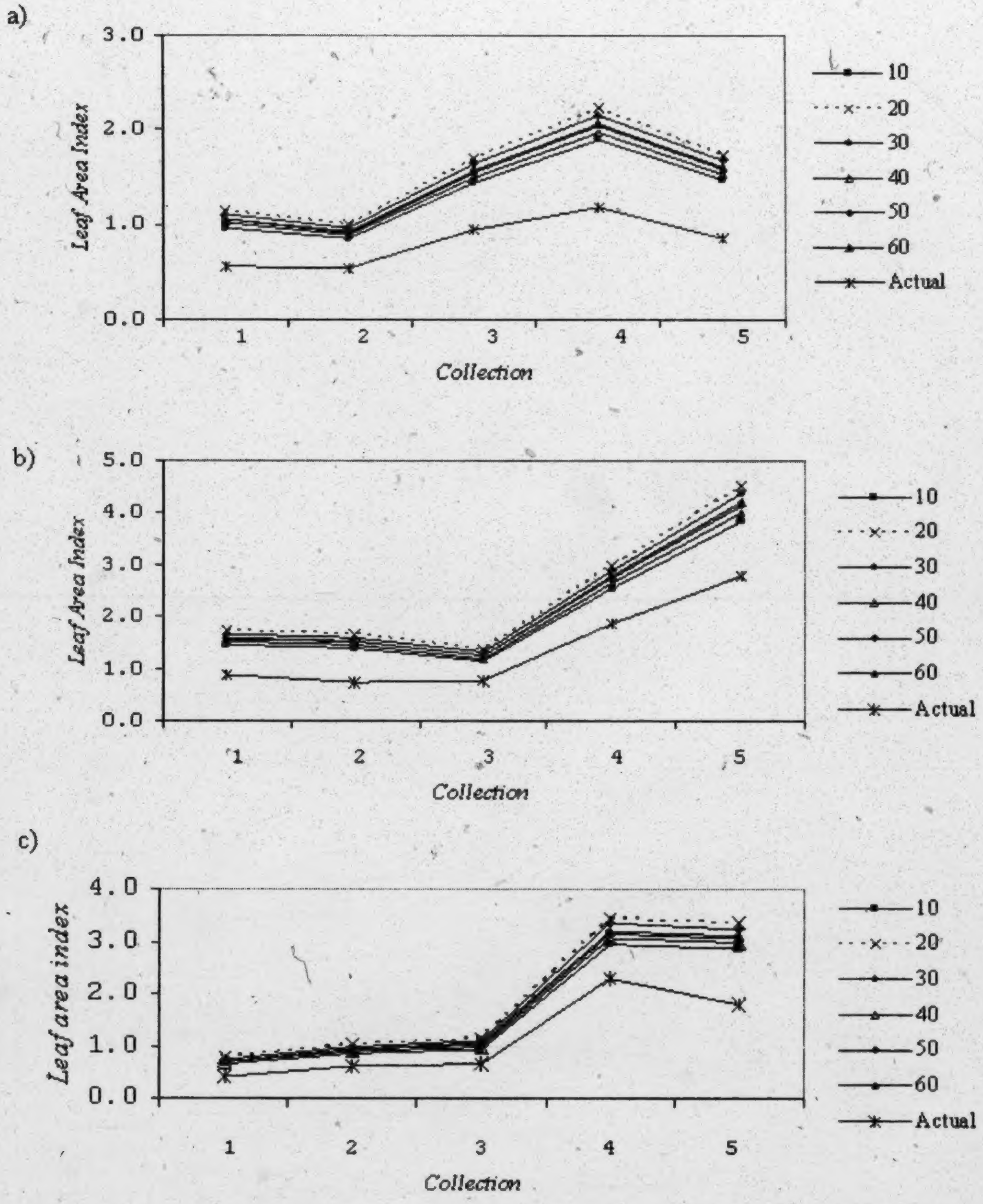


Figure 3.4. Cumulative number of species observed per cumulative number of traps based on 500 randomizations and estimates from the Incidence Based Estimator (ICE). a) early stage, b)intermediate stage and c) late stage

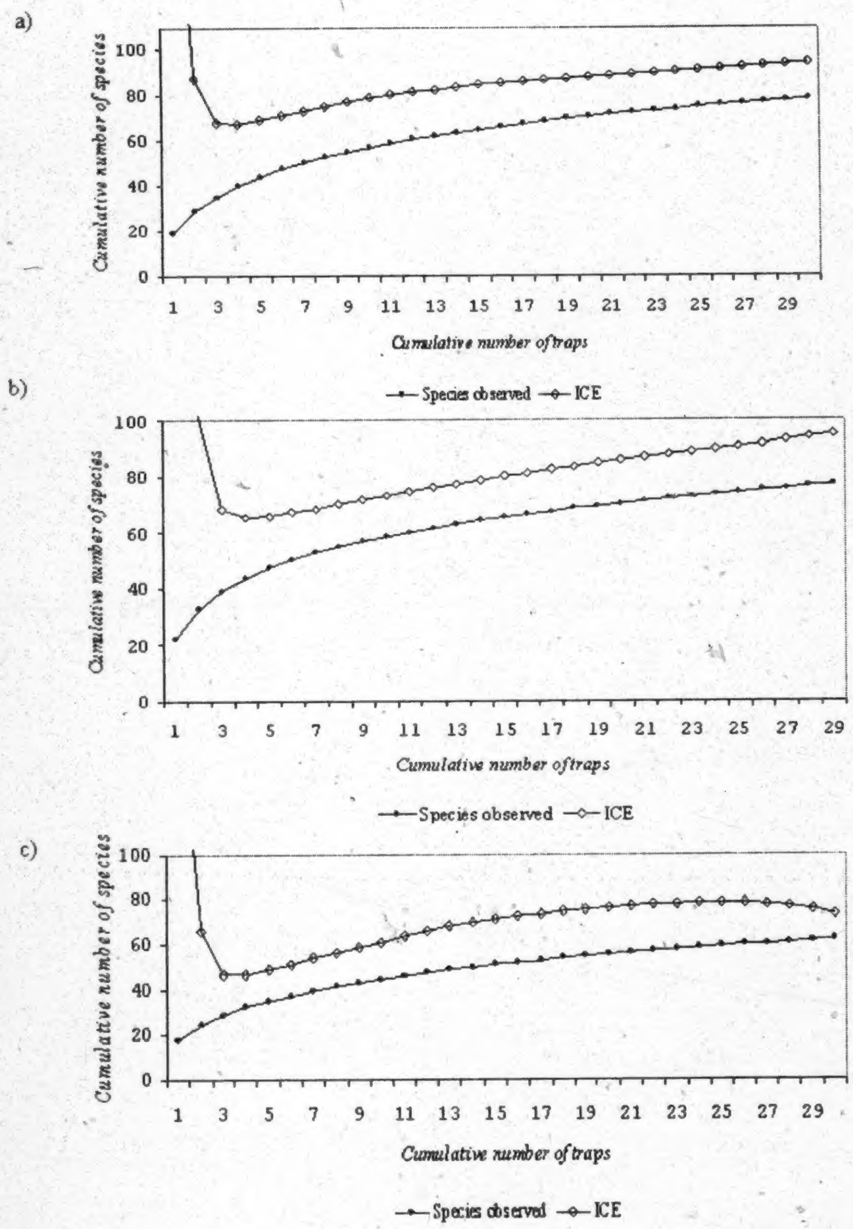


Figure 3.5. LAI values using mean SLA values (10-60 species) compared to actual LAI values using unique SLA values for each species. a) early stage, b) intermediate stage, c) late stage

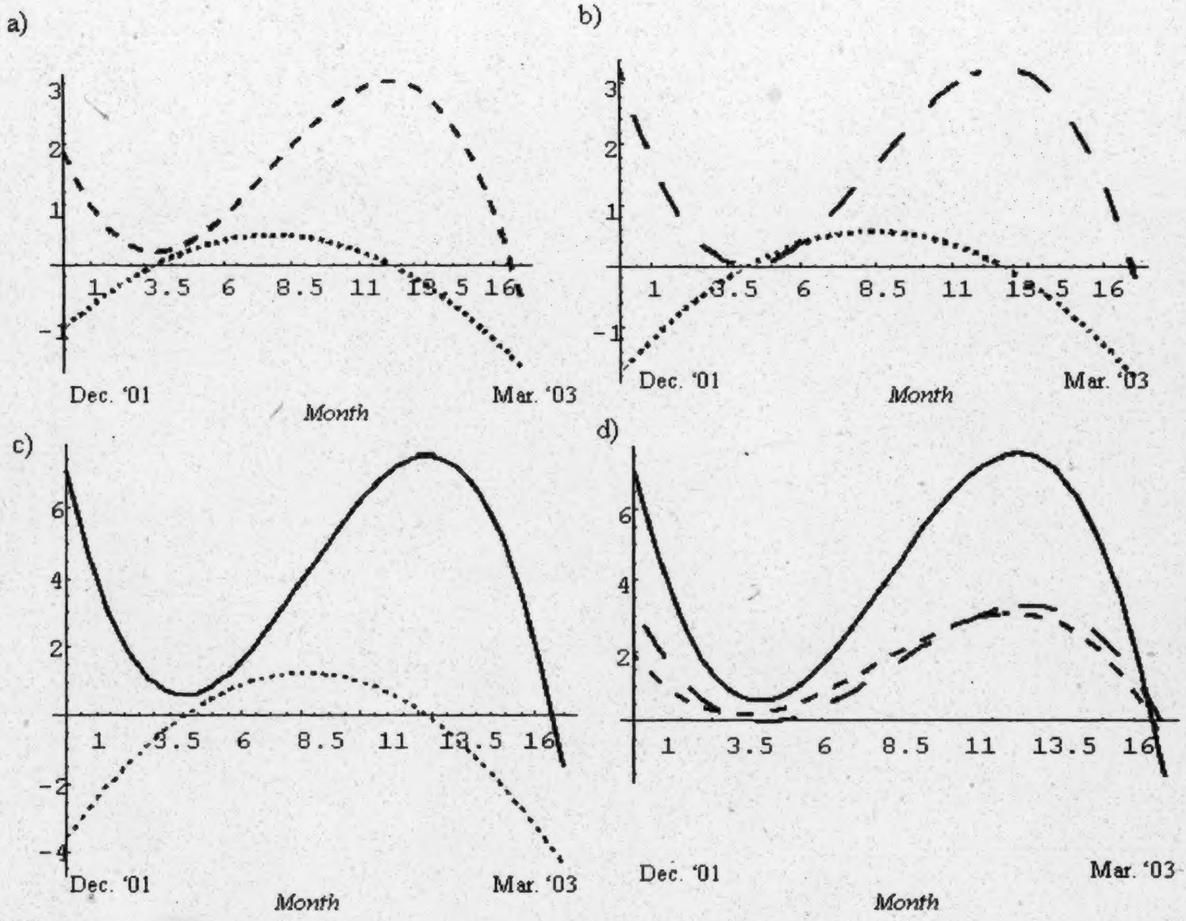


Figure 3.6. Third order polynomial function of the seasonal trend in LAI and the first derivative (fine dashing) indicating the months with the minimum and maximum LAI values (points where first derivative crosses X-axis) a) early stage b) intermediate stage c) late and d) Seasonal LAI from calibrated LAI-2000 estimates. Solid line indicates the late stage, the long dashing the intermediate stage and then short dashing the early stage.

Chapter 4: Estimating leaf area index from satellite imagery using Bayesian Networks[1]

4-1. Introduction

The computer-based interpretation of remotely sensed image data typically involves models and algorithms that are capable of combining evidence from what is being sensed (the spectral signature) with prior knowledge. This prior knowledge resides in what is known about the sensors, the surfaces (or types of vegetation canopies), objects and terrains being sensed. Predicting the leaf area index (LAI) for specific terrains from remotely sensed images is an example of such a task. Graphical Models and, in particular, Bayesian Networks (BN) provide a useful way of dealing with such problems because they combine the robustness of probabilistic methods with the expressiveness of graphs that encode relationships between variables and, as such, offer a framework for handling uncertainty and complexity in decision-support systems within a single model (Jordan 1999). Specifically, Graphical Models represent the complex interactions between variables in terms of their individual probability densities and their dependencies as defined by contingency tables.

BNs have often been employed in medicine, forensic sciences, economics, computer vision, image processing and the artificial intelligence communities (Stassopoulou and Caelli 2000, Biedermann et al. 2004, among many others) with significant success. However, their popularity in combining ecological questions with satellite remote sensing studies is limited in comparison (Kiiveri et al. 2001). In this paper we introduce a new approach for estimating an ecological variable, LAI, from satellite imagery using Bayesian Networks.

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4-1.1. Leaf Area Index and Remotely Sensed Data

The LAI, half the total surface area per unit of horizontal surface, is an important variable in many process-based models for forest ecosystems (Running and Coughan 1988, Landsberg and Waring 1997). It is one of the most dynamic components of the forest canopy which is especially evident in areas with strong seasonal leaf phenology. Leaves have also been found to be the most adaptable component of the canopy in their response to changes in environmental conditions (Welles 1990). In areas with a deciduous broad leaf canopy such as the tropical dry forest, the majority of the woody species lose their leaves during the prolonged dry seasons (Gentry 1995).

LAI has often been linked to remotely sensed data empirically through the use of spectral vegetation indices (SVI) with variable degrees of success (Hall et al. 1995, Fournier et al. 2003, Kalacska et al. 2004a, Chapter 5). SVIs are calculated from various spectral bands of airborne or space-borne remotely sensed imagery. They are designed to exploit characteristic reflectance properties of vegetation. The two regions of the electromagnetic spectrum used most often for SVIs are the red and near infrared wavelengths. Green vegetation is highly reflective and transmissive in the near infrared (0.75-1.35 μm) and highly absorptive in the red wavelengths (0.62-0.75μm) (Gates 1965). By exploiting this difference, SVIs can be related to leaf properties (Verstraete and Pinty 1996). A drawback to this approach, however, is that saturation in the individual wavelength regions has led to saturation in the SVIs at LAI values anywhere from 3 to 8 resulting in the loss of sensitivity to changes in LAI (Birky 2001, Kalacska et al. 2004a). The actual point of saturation is ecosystem dependent. This is highlighted by a large scale study in Canadian ecosystems where using the infrared simple ratio (ISR) (Landsat band 4/Landsat band 5) (Birky 2001) did not find that ISR saturated even at LAI values above eight. Recently such difference or ratio measurements have been replaced by methods that use non-linear spectral evaluation methods such as radiative transfer models as well as neural networks, statistical classifiers to estimate LAI from remotely sensed data (Fang et al. 2003, Fernandes et al. 2003, Atzberger 2004, Walthall et al. 2004 among many others).

Classification approaches have the benefit of summarizing variability in data as well as deriving classification rules under uncertainty. However, they lack in explanatory power: how the known variables, and their dependencies explain given LAI values. Bayesian Networks provide such a framework to evaluate such causal models while retaining the probabilistic and statistical benefits of classification models. We compare the results of this approach to a LAI-SVI model and a Neural Network Classifier. However, before doing so a brief introduction to BNs is provided in the following section.

4-1.2 Basic Principles of Bayesian Networks

A Bayesian Network (BNs, also known as a belief, probabilistic or causal network) is a directed acyclic graph (i.e. no cycles) that models the dependencies between variables in the probability model and has the ability to perform inference concerning variable states given the states of other variables and observations. This enables the use of probabilistic and statistical methods for reasoning in situations with uncertainty and describing a multivariate probability distribution function over a set of random variables (Sivia 1996).

A BN is composed of a set of random variables (also known as vertices or nodes) with directional links (edges, arcs) between them (directed graph) denoting a conditional relationship (Pearl 1988, Pearl 2000, Jensen 2001, Murphy n.d.). The variables (if continuous) need not be normally distributed (Jordan 1999). The links may represent causal or simple dependencies depending on the application. The relationships between the nodes are referred to by kinship terms (i.e. parents, children, ancestors, etc.) and are quantified by conditional probability tables (CPTs). For example, a node A with parents $B_1 ... B_n$ will have a CPT of: $P(A|B_1 \ldots B_n)$. Nodes with no parents (i.e. root nodes) with states $x_1 \ldots x_n$ have a discrete probability distribution over $x_1 \ldots x_n$ such that

$$\sum_{i=1}^{n} x_i = 1 \tag{1}$$

and where $x_i \geq 0$ with the probability of X being in the state x_i is $P(X=x_i)$. The conditional dependence and independence of nodes in a graphical model allow for substantial simplification of joint probabilities (Murphy n.d., Wikepedia n.d.). For example, specifying the joint multivariate distribution $P(X_1 \ldots X_n)$ for n two-state variables requires a table with 2^n entries. However, that can be greatly reduced if this multivariate distribution depends only on a subset of the variables – the basis for BNs. That is, a BN corresponding to the joint probability of all nodes $X_1 \ldots X_n$ decomposed as the product of n conditional distributions is (Pearl 1988, Pearl 2000, Murphy n.d.):

$$P(X_1..X_n) = \prod_j P(X_j / pa_j) \tag{2}$$

where pa_j correspond to the parent variables of X_j- the variables X_j is dependent upon. Each such dependency is defined by the CPT that quantifies the relationships between the nodes of the network. Node random variables within a BN can be discrete (as in this case), or continuous, and there cannot exist cycles of dependencies within the network (Jensen 2001). For inference, it is necessary to have estimates of these underlying probabilities in the form of contingency tables or individual node probability densities. Here, we use a combination of direct model estimates from data and current model refinement methods to estimate conditional probability values using the Expectation Maximization algorithm. Given model estimates we then use optimal inference methods to infer variable states and, in particular, predict LAI values from other variable values. A Naïve Bayesian classifier, a simple form of a Bayesian Network, assumes independence between parent nodes and is substantially robust to violations of such assumptions (Wikepedia n.d.). Accordingly, a Bayesian Net based on a conditional independent Naïve Bayes model substantially simplifies calculations while remaining robust.

4-1.3 Bayesian Networks vs. Neural Network Approaches

Another recent type of classifier used for LAI is a Neural Network and it is important to note the differences between BNs and Neural Networks. First, in a

BN all nodes are explicitly defined along with their dependencies. For a Neural Network, the hidden nodes are not directly defined but they are estimated in order to summarize specific types of attribute dependencies inherent in the input, or input-output, relations, so providing the basic for classification rules. Secondly, and most importantly, inference techniques have been developed for BNs which are provably optimal as opposed to Neural Networks where estimations of the network weights that define the characteristics of the hidden units and classifications are approximate (locally optimal due to the use of gradient-based optimization methods) and subject to over- or under-fitting. Albeit, Neural Networks have proved useful as a classification approach for identifying different LAI states.

The most common inference method for BNs is the Junction Tree (JT) algorithm (Jensen 1999) that allows us to propagate probabilities and combine evidence to answer queries about relationships between variables and their specific states within the BN. This algorithm is based on the extraction of cliques (maximal complete subgraphs) of variables within the BN that contain evidence about clique member dependencies and propagates this to other cliques in such a way that allows us to draw conclusions that are MAP (Maximum posterior probability), given the data and BN model(Jensen 1999).

Here we explore how Bayesian Networks can be applied to the optimal inference of LAI for remotely sensed images and compare it with the performance of an SVI and a Neural Network classifier.

4-2. Methods

4-2.1 Model description

4-2.1.1Data Description

LAI and forest structure data were collected in the Santa Rosa National Park in the Área de Conservación Guanacaste NW Costa Rica (10° 48' 53", -85 ° 36' 54"). The area is composed of a matrix of secondary dry forest in various stages of regeneration and mature forest that has suffered only some degree of anthropogenic disturbance. We refer to three stages of succession: early, intermediate and late which have been shown to have an asynchronous leaf phenology (Kalacska et al. 2004b, Chapter 3). The majority of the park is comprised of uplands which are relatively flat (~250m a.s.l). Canyons and slopes are present towards the south-west as the park descends to sea level. Plant area index (PAI) was estimated optically in April (dry season) and November (wet season) with the LAI- 2000 Plant Canopy Analyzer (PCA) from LI-COR Inc. according to the sampling scheme described in (Chapter 3). PAI was subsequently converted to true LAI by applying the calibration equations described in Chapter 3 that were developed from litter traps.

In total, we included forest structure and LAI data from 16 plots (30x60m – 0.18ha) covering the range of the three stages. The forest structure data consisted of mean canopy height (H) (7.5 - 15m), basal area (G) (11.7 – 30.1m^2/ha), stem density (D) (107 – 130 stems/0.1ha) and species density (S) (15 - 29 species/0.1ha) (Kalacska et al. 2004b). The range for the calibrated LAI in the dry season was 0.0 – 3.7. Mean values (±σ) for the three stages were (in order): 0.4±0.7, 0.4±1.0 and 1.5±1.9. For the wet season, the range is 0.5 – 15 where the mean values for the three stages were: 3.8±2.5, 3.7±1.9, and 11.3±4.8.

The satellite images used in this analysis are Landsat 7 ETM+ images (28.5m spatial resolution) (Path 16, Row 52) acquired in November 2001 and April 2002. The images were orthorectified to a UTM Zone 16N. WGS84 projection. Digital numbers were converted to surface reflectance with ATCOR2 using a standard tropical rural atmosphere model which takes into consideration the differences in solar elevation and image acquisition time of day and date (ATCOR n.d.). We use surface reflectance rather than radiance or top of the atmosphere reflectance because surface reflectance has been found to have the best empirical relationships with LAI (Turner et al. 1999). The reflectance values from bands 1-5 and 7 were extracted from the images in a 3x3 pixel window around the centre of each plot. A vegetation index, NDVI (Normalized Difference Vegetation Index) was subsequently calculated from the red and near infrared spectral bands. In order to predict successional stage NDVI was used in place of other SVIs because it has been shown that in our study area it statistically discriminates the best between the stages (Arroyo-Mora et al. 2005). Figure 4.1 illustrates the mean and one standard deviation of LAI and the red and near infrared reflectance bands for each stage as a function of season. The differences seen in the LAI data are supported by the structural variables (Kalacska et al. 2004b). The higher values of NIR reflectance in the dry season are due to the increased contribution of woody matter, leaf litter, dry grass and soil which have a higher reflectance in the NIR.

4-2.1.2Bayesian Network

To avoid overfitting, we sought to construct a network with the simplest topology which still had the ability to infer LAI with an acceptable error rate. The final Bayesian Network was composed of nine nodes (Figure 4.2) defining the basic set of variables of interest. The structure and stage nodes are variables that influence LAI in this ecosystem (Chapter 5). The reflectance nodes are those that are sensitive to changes in LAI. NDVI while not conducive to estimate LAI, is sensitive to the differences in reflectance between the successional stages (Arroyo-Mora et al. 2005).

A summary of the nodes can be found in Table 4.1. The number of states for ND, R3 and R4 was chosen based on a set of tests (4 – 8 states) to improve the overall accuracy of the network. Nodes R3, R4 and ND are instantiated during inference. The last bin of the LAI node includes all values greater than six. The number of states for LAI was chosen as a compromise between precision and accuracy. The BNs were constructed and compiled with Netica v.2.17and were run on every pixel of the Landsat 7 ETM+ images using the Java version of Netica implemented in Matlab v.6.5. In the final model described here only the red and near infrared bands are used. Initially, other bands (e.g. bands 5 and 7) were included in the BN. However, as the performance of the network was evaluated with various band combinations, the best result was obtained with those two bands (e.g. including others such as band 5 or 7 resulted in an error > 60% in the wet season).

4-2.1.3 Training and image processing

Since BNs allow propagation of information in the form of instantiated variable states forward or backward through nodes, BNs allow both deductions and abductions. From Bayes rule, the posterior distribution, g, is estimated by

$$g(\theta \mid x_1..x_n) = \frac{f(\underline{x}/\theta)g(\theta)}{f(\underline{x})} \qquad (3)$$

where $f(\underline{x})$ is the marginal likelihood of the sample $\underline{x}=(x_1 \ldots x_n)$ (Blackmond-Laskey n.d.).

The models were trained with data sets consisting of 108 cases per season (random selection from the 144 pixels – 9x9 pixel window from the 16 independent plots). The conditional probability tables (CPTs) were then estimated using the Expectation-Maximization (EM) algorithm (Jensen 1999) that updates initial parameter estimates by iteratively refitting the data to the updated model till convergence (using the NETICA BN software package). The two assumptions of the algorithm are that the conditional probabilities that are being estimated are independent and that the prior distributions are assumed to be multinomial (Norsys 1998).

The resultant models were applied at the pixel level to the Landsat 7 ETM+ images. The Junction Tree algorithm was then used for exact probabilistic inference. Table 4.2 describes the cliques of the junction tree. The steps of the Junction Tree algorithm are summarized as follows (Jensen 1999): The first step in the Junction tree algorithm is to moralize the graph – a process where links are added between non-adjacent parents of the same child. The second step is to replace directional links with non-directional links. The third, and somewhat complicated, step is to triangulate the graph. A triangulated (chordal) graph is one with no chordless cycles. That is, a graph where all cycles of length greater than 3 contains at least one edge between a pair of non-adjacent vertices. The fourth step involves the conversion of the triangulated graph into a clique graph. This graph is a hypergraph where each clique (for example, each triangle of connected vertices) is defined as a vertex in the clique graph. The Junction Tree is a subset of the clique graph that is both a tree, by choosing a root clique, and satisfies the following condition: for each pair of cliques (A and B) with an intersection (T), all the cliques on the path between A and B contain T. Once defined, the algorithm when running, assigns the conditional probability tables in the original BN associated with the clique nodes that contains all the variables referenced by the table. Once done, the product of the distributions is taken and this process is repeated until all the nodes are eliminated. The Junction Tree algorithm is a generalization of dynamic programming as used in hidden Markov models for determining MAP estimates of the most likely state sequences given data and the model as it runs over the Junction Trees generated from the chordal, trianguated, graph version of the original BN model (Jensen 1999).

Once such networks (Figure 4.2) were compiled into junction trees, they could be queried via observation values for nodes ND, R3 and R4. Belief updating was computed for the other nodes by a message passing algorithm that operates using the junction tree (Norsys 1998). The probability density functions are adjusted in order to achieve the maximum likelihood of the model states compared to the node distribution values estimated from the training data. Subsequently, the state for L with the highest probability is extracted along with the value of its probability. The preceding steps were computed for each pixel of the image and the result is two new images, one of the LAI states with the highest probabilities (LAI map) and one of the probabilities of the LAI values predicted (Figure 4.3).

4-3. Results

4-3.1 Network testing

The BNs were tested on a random subset of 36 cases (pixels) per season that were not used in the learning process. The error rate, RMSE and scoring rule results are listed in Table 4.3. In general, scoring rules provide an evaluation of predicted probabilities of states over a set of variables (Colwell et al. 1993). Three more common scoring rules are, one, logarithmic loss (Norsys 1998):

$$\mathrm{M}\left(-\log(P_c)\right) \tag{4}$$

where M is the mean over all test cases and P_c is the probability of the correct state; two, quadratic loss (Norsys 1998):

$$\mathrm{M}(1 - 2 \times P_c + \sum_{j=1}^{n} P_j^2) \tag{5}$$

where P_j is the probability of the predicted state and n is the number of states and three, spherical payoff (Norsys 1998):

$$M\left[\frac{P_c}{\sqrt{\sum_{j=1}^{n} P_j^2}}\right] \qquad (6)$$

The logarithmic loss is the only scoring rule whose value is determined solely by the probability of the outcome that actually occurs (Colwell et al. 1993). For logarithmic loss (0 to ∞) and quadratic loss (0 to 2), scores close to zero are better. For spherical payoff (0 to 1) 1 is the best. Consistently the dry season model outperformed the wet season model (e.g. 17.6 vs. 48.7% error rate and RMSE of 1.6 vs. 1.9). The dry season network also received better scores for each of the scoring rules than the wet season image (Table 4.3).

Calibration scores which evaluate the confidence expressed by the network, indicate that for the dry season in at least 75 - 86% of the test cases the network was correct in its predictions when it had high confidence in the most likely state. For the wet season, the network was correct up to 71% of the time when it was highly confident in the most likely state. When the 'times surprised' is evaluated the dry season network had a range of 0 – 11% and the wet season network a range of 0 – 1%. This is a measure of the network being incorrect when it was highly confident either that a particular state is likely or unlikely (i.e. 90-99% probable or 1-10% probable) (Norsys 1998). Eleven percent of the time when the dry season network was highly confident in its prediction (i.e. >90%), it was actually incorrect in its prediction. When the network had a predicted probability < 10%, it was "surprised" on average 1.8% of the time with that state actually being the correct one. The wet season network rarely made strong predictions but on the instances where it did the predicted state was correct. On average 10% of the time its predictions with less than 3% confidence were correct, and 5% of the time its predictions with less than 1% predicted probability were correct.

4-3.2 Comparison with spectral vegetation index and a neural network classifier

For the wet season image (full foliage image) we compare the BN-LAI approach with a more traditional LAI-SVI approach as documented in (Chapter 5). Of the four vegetation indices (NDVI, SR, MSR, SAVI2) calculated, SAVI2 had the strongest relationship with LAI with a transition function, the Lorentzian Cumulative model (Adj. R^2=0.71, P=0.001) (Kalacska et al. 2004a). The overall error rate and RMSE for this LAI-SVI model was calculated from the same validation data set as used for the BN. The results shown in the LAI-SVI model had a lower RMSE than the BN (1.5 vs. 1.9) but a higher overall error rate (64.9% vs. 48.7%).

We also compare the results from the wet season image to a neural network classifier model. Using the same spectral bands and NDVI (same inputs as the instantiated nodes in the BN) we trained and tested a neural network classifier in PRTools v.3.0 for Matlab (Duin 2000). The network had, again, the same observation sets as the BN and three hidden units were found to have best classification performance which, in general, was inferior to that of the BN. Adding additional hidden layers (i.e. 4 to 8 layers) the testing error increased to over 60%. The standard back propagation algorithm was used for training the network and classification was based on the class with the highest output. The resultant errors (with three hidden layers) were: 42.4% (training) and 56.9% (testing) compared to a total error rate (testing error) of 48.7% for the BN.

4-4. Discussion

In this analysis we have demonstrated a novel approach to estimating LAI from remotely sensed data. Bayesian Networks allow for the revision and updating of prior beliefs with the addition of new evidence (field data). They also allow for a relative view about the state of knowledge of a given ecosystem rather than an absolute view because the beliefs are continuously updated with increasing knowledge permitting insight into complex problems (Biedermann et al. 2004). Of particular importance is that they provide a model for combining and reasoning about evidence from quite different sources and measurement types.

Overall, the dry season network performed much better than the wet season network for all ranges of LAI values. While it had the greatest confidence in its predictions in areas where LAI values are low (< 3) the confidence in its predictions in areas with higher LAI area acceptable. The increased confidence in areas with low LAI is partly due to the training data in which the majority of the cases had LAI values below 3. However, this was because in the study area, the early and intermediate stages comprise 59% of the total area. The late stage comprises 27% and the remaining 12% is composed of pastures (not of interest in this study) (Arroyo-Mora et al. 2005). The early and intermediate stages have characteristically low LAI in the dry season (Figure 4.1). The lower confidence in predictions for LAI greater than 3 did not affect the accuracy or predictive power of the BN (Table 4.3). Only six cases (out of 36) were misclassified in the validation data set (Figure 4.4). The confusion (also manifested in the surprise index) seems to be mainly due to the areas of intermediate succession which have the greatest variability in their spectral signature and, in many cases, resembling either the early or late stages in the dry season (Figure 4.1) (Arroyo-Mora et al. 2005).

In the wet season the differences in spectral reflectance seen in the dry season are slight to minimal (Figure 4.1). In addition, the confidence of the network in its predictions is lower in the entire image compared to the dry season. In the early stage, the ground is covered with a thick inhibitory grass/herb layer (up to 2m tall) which in addition to the green tree canopy of this stage has a reflectance signature very similar and sometimes equal to (or greater than in extreme cases) the canopy signatures of more mature stages. In the intermediate stage (and sometimes the early stage), the canopy in many areas has a high presence of lianas (non self supporting climbers) along with a dense canopy that resembles the late stage. Yet, while the three stages have very similar spectral signatures, differences do exist in field estimates of LAI (Figure 4.1). In the late stage for example, the canopy is multistratal with up to two canopy tree layers whereas in the early and intermediate stages there is only one canopy tree stratum (Kalacska et al. 2004b). In addition, in the early stage the grass/herb layer is not sensed by the PCA during the LAI estimation. But because these differences are not mirrored by the reflectance data, the power of the network is compromised as seen in the higher error rate and RMSE as well as the poor scoring rule results (Table 4.3, Figure 4.4).

In comparison to the LAI-SVI method, the BN had a lower total error rate, but slightly higher RMSE. Similarly, the error rate for the neural network classifier was higher than that of the BN. The sources for confusion (e.g. similarity in spectral signatures between forest and open areas with tall grass) are the same for the all models, at least at this spectral and spatial resolution. A potential drawback to the LAI-SVI method presented in Chapter 5 is that a single SVI (SAVI2) was used for each stage. In the future, with additional data it would be possible to construct separate regression models for each stage and possibly improve the model.

For future improvements of both BN models (but especially the wet season model) we recommend the use of a finer spectral resolution image where subtle differences in spectral signature of areas with different LAI not inherent in the Landsat 7 ETM+ image would likely be more apparent. The number of bands to choose from would also be advantageous (Lee et al. 2004). Also, the addition of random noise to the training data may help the model have more accurate predictions in areas that are not included in the training set.

The inclusion of the structure nodes (while ancillary for this classification) allows for the inference of LAI based on the instantiation of those four nodes if at a future time addition structure data (with out LAI) became available. While not explored in this analysis, we predict that the results would be a broader classification of LAI than with the instantiation of the reflectance nodes (shown in this study). In order for this BN in order to predict LAI, successional stages are more important than structural variables. In this ecosystem successional stage can be rapidly estimated in the field or alternatively from NDVI values (Kalacska et al. 2004b, Arroyo-Mora et al. 2005), therefore, for future implementation of the model the structural variables are not explicitly required. An additional consideration for this model is the discretization of successional stages. While it has been shown by (Kalacska et al. 2004b) that the variables that encompass the forest structure of the stages in this study area are statistically distinct, successional stages are in fact continuous. It is possible that pixels which represent forest in the overlapping regions of two stages add uncertainty to this and other models which include successional stage as a variable. For other ecosystems, individual models can be developed which take into account the unique characteristics of the ecosystem and the factors that influence reflectance. We stress that models (empirical, probabilistic, etc.) must be evaluated on an ecosystem basis. Differences in land cover or forest structure will pose unique challenges that are particular to each type of ecosystem, therefore, models developed in one cannot be directly transferred to another. Nor can the error rate of a particular model in an ecosystem be compared to a different model in a different ecosystem.

In other ecosystems, the inversion of radiative transfer models such as look-up-tables or artificial neural networks have proven to be highly successful. Through the examination of these techniques certain drawbacks regarding the nature of the inversion problem have been highlighted. For example, (Baret and

Guyot 1991) state that depending on the leaf orientation, the spectra of certain sparse and dense canopies may be very similar. Others have reinforced the errors associated with the simplification of the scattering behaviour of leaves (Atzberger 2004). By not considering the effects of neighbouring pixels the errors of such assumptions may become compounded as the spectral signature of each pixel is affected by its neighbours. This also reinforces the need to develop or customize any model for the specific ecosystem it is being used in which as much specific information on the nature of the canopy is taken into consideration.

Bayesian Networks utilize explicit probabilistic relationships between variables and so their robustness and reliability depend on the quality of the learning data and prior distribution estimation methods. A representative sample of the possible states is required in order for the model to learn the CPTs adequately. The precision and accuracy of the models rely on both the strength of the pattern inherent in the training data and the quality of such data. The variability in the predictions of the networks can be seen as a measure of their strength and sensitivity in representing the uncertainty in the represented relationships (Taroni et al. 2004).

4-5. References

Arroyo-Mora J.P., Sanchez-Azofeifa G.A., Rivard B., Calvo-Alvarado J.C., Kalacska M., Janzen D.H. 2005. Secondary forest detection in a Neotropical dry forest: complementary use of IKONOS and Landsat 7 ETM+ imagery. *Biotropica*, vol. 37, pp.498-507.

Atzberger C., "Object-based retrieval of biophysical canopy variables using artificial neural nets and radiative transfer models" *Remote Sensing of Environment*, vol. 93, pp. 53-67. 2004

Baret F., Guyot G. “Potentials and limits of vegetation indices for LAI and APAR assessment” *Remote Sensing of Environment*, vol. 91 pp. 161-173. 1991.

Biedermann A., F. Taroni, O. Delemnot, C. Semadeni and A. C. Davison, “The evaluation of evidence in the forensic investigation of fire incidents (Part I): an approach using Bayesian networks,” *Forensic Science International*, in press, 2004.

Birky A., “NDVI and a simple model of deciduous forest seasonal dynamics”, *Ecological Modeling* vol. 143, pp. 43-58. 2001.

Caelli T., Bischof W.T. *Machine Learning and Image Interpretation (Advances in Computer Vision and Machine Intelligence)*. New York: Plenum, 1997.

Colwell R.G., Dawid A.P., Speigelhalter, “Sequential model criticism in probabilistic expert systems”, *IEEE Trans. Pattern Anal. Mach. Intell.*, vol. 77, no. 3, pp. 209-219, Mar. 1993.

Dawid A.P. “The well-calibrated Bayesian: A rejoinder” *J. American Statis. Assoc.*, vol. 77, pp-612-613, 1982.

Duin R.P.W. “PRTools Version 3.0: A Matlab toolbox for pattern recognition” Pattern Recognition Group, Delft Univ. Technology, Delft, The Netherlands, 2000.

Hall F.G., Townshend J.R., Engman E.T. “Status of remote sensing algorithms for the estimation of land surface state parameters” *Remote Sensing Environment* vol. 51, pp.138-156, 1995.

Fang H., Liang S., Kuusk A., “Retrieving leaf area index using a genetic algorithm with a canopy radiative transfer model”, *Remote Sensing of Environment*, vol. 85, pp. 257-270. 2003.

Fernandes R., Butson C., Leblanc S., Latifovic R. “Landsat-5 TM and Landsat-7 ETM+ based accuracy assessment of leaf area index products for Canada derived from SPOT-4 VEGETATION data” *Canadian Journal of Remote Sensing* vol 29, pp.241-258. 2003.

Fournier R.A., Mailly D., Walter J.-M., Soudani K. “Indirect measurement of forest canopy structure from in situ optical sensors” in *Methods for remote sensing of forests: Concepts and case studies* M. Wulder and S. Franklin Eds. Netherlands:Kluwer Academic Press pp. 77-114, 2003.

Gates D.M. “Spectral properties of plants” *Applied Optics* vol 4, pp. 11-20, 1965

M.M. Verstraete and B. Pinty, "Designing optimal spectral indexes for remote sensing applications", *IEEE Transactions of Geosciences and Remote Sensing*, vol. 34, pp. 1254-1265, 1996.

Gentry A.H., "Diversity of floristic composition of Neotropical dry forests" in *Seasonally dry tropical forests*, H.A. Mooney, S.H. Bullock and E. Medina. Eds. Cambridge: Cambridge University Press, 1995, pp.146-194

Jensen F.V., *Bayesian Networks and Decision Graphs* New York: Springer-Verlag , 2001.

Jordan M.I. *Learning in Graphical Models* Massachusetts: MIT Press. 1999.

Kalacska M., Sanchez-Azofeifa G.A., Rivard B., Calvo-Alvarado J.C., Journet A.R.P., Arroyo-Mora J.P., Ortiz-Ortiz D. "Leaf area index measurements in a tropical moist forest: A case study from Costa Rica", *Remote Sensing of Environment* vol 91, pp.134-152, 2004a.

Kalacska M., Sanchez-Azofeifa G.A., Calvo-Alvarado J.C. Quesada M., Rivard B., Janzen D.H, "Species composition, similarity and diversity in three successional stages of a seasonally dry tropical forest" *Forest Ecol. Manag.*. vol. 200, pp. 227-247, 2004b.

Kalacska M., Calvo-Alvarado J.C., Sanchez-Azofeifa G.A, "Calibration and assessment of seasonal changes in leaf area index of a tropical dry forest in different stages of succession," *Tree Physiol.* vol. 25, pp. 733-744, 2005a.

Kalacska M., Sanchez-Azofeifa G.A., Calvo-Alvarado J.C., Rivard B., Quesada M. "Effects of seasonal and successional stage on leaf area index and spectral vegetation indices in three Mesoamerican tropical dry forests" *Biotropica*, vol 37 pp. 486-496 2005b.

Kiiveri H.T., Caccetta P., Evans F.. "Use of conditional probability networks for environmental monitoring" *International Journal of Remote Sensing*. vol. 22, pp.1173-1190. 2001.

Landsberg J.J. Waring R.H., "A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning" *Forest Ecology and Management*, vol 95, pp. 209-228, 1997.

Lee K.-S., Cohen W.B., Kennedy R.E., Maiersperger, Gower S. T. "Hyperspectral versus multispectral data for estimating leaf area index in four different biomes" *Remote Sensing of Environment*, vol. 91, pp.508-520, 2004.

Murphy K., "An Introduction to graphical models" Unpublished.

Netica. Norsys Software Corp., Vancouver BC, Canada. Available online at: http://www.norsys.com 1998.

Pearl J., *Probabilistic Reasoning in Intelligent Systems: Networks and Plausible Inference* San Francisco: Morgan Kaufman Publishers, 1988.

Pearl J., *Causality* New York: Cambridge University Press, 2000.

Running S.W., Coughan J.C., "A general model of forest ecosystem processes for regional applications I: Hydrologic balance, canopy gas exchange and primary production processes" *Ecological Modeling*, vol. 42, pp.125-154, 1988.

Sivia D.S., *Data Analysis a Bayesian Tutorial.* Oxford: Clarendon Press, 1996, ch. 1.

Stassopoulou A., Caelli T., "Building detection using Bayesian Networks", *International Journal of Pattern Recognition and Artificial Intelligence*, vol 14 pp. 715-733, 2000.

Taroni F. Biedermann A., Gabolino P. Aitken C.G.G. "A general approach to Bayesian networks for the interpretation of evidence" *Forensic Science International*, vol. 139, pp.-5-16, 2004.

Turner D.P., Cohen W.B., Kennedy R.E., Fassnacht K.S., Briggs J.M, "Relationships between leaf area index and Landsat TM spectral vegetation indices across three temperate zone sites," *Remote Sensing of Environment*, vol. 70, pp. 52-68, 1999.

Verstraete M.M., Pinty B. "Designing optimal spectral indexes for remote sensing applications", *IEEE Trans. Geosci. Remote Sens.* vol. 34, no. 5, pp-1254-1265, Sept. 1996.

Walthall C., Dulaney W., Anderson M., Norman J., Fang H., Liang S., "A comparison of empirical and neural network approaches for estimating corn and soybean leaf area index from Landsat ETM+ imagery", *Remote Sensing of Environment*, vol 92, pp.465-474, 2004.

Welles J.M., "Some indirect methods of estimating canopy structure", *Remote Sensing Reviews,* vol 5, pp. 31-43, 1990.

Wikepedia Online Encyclopedia. "Naïve Bayesian classification" Unpublished. Available online: http://en.wikepedia.org/wiki/Naive_Bayesian_classification

Table 4.1Node definitions and probabilities

Node	Definition	Type	(Un)conditional Probability	No. bins
H	Tree height (m)	DC.R	$P(H \mid ST)$	10
G	Basal area (m^2/ 0.1 ha)	DC.R	$P(G \mid ST)$	10
D	Stem density (No./0.1 ha)	DC.R	$P(D \mid ST)$	10
S	Species density (No./0.1ha)	DC.R	$P(S \mid ST)$	10
ND	NDVI – Normalized Difference Vegetation Index	DC.R	$P(ND)$	dry: 3 wet: 5
R3	Red reflectance (Landsat 7 ETM+ band 3)	DC.R	$P(R3)$	dry: 6 wet: 8
R4	Near infrared reflectance (Landsat 7 ETM+ band 4)	DC.R	$P(R4)$	dry: 6 wet: 8
ST	Successional stage	D	$P(ST \mid ND)$	3
L	Leaf Area Index	DC	$P(L \mid ST.R3.R4)$	7

DC = Discretized Continuous. D = Discrete. R = Root node: dry = dry season. wet=wet season

Table 4.2Junction tree cliques for the Bayesian Networks

Clique	Joined to	Size	Member nodes
0	1	12	ND, ST
1	0,2	30	ST, D
2	1,3,5	24	L, ST
3	2,4	48	R3, L
4	3	48	R4, L
5	2,6	30	H, ST
6	5,7	30	G, ST
7	6	33	S, ST

Table 4.3 Bayesian Network performance

Season	Error Rate (%)	RMSE	Logarithmic Loss	Quadratic Loss	Spherical Payoff
Dry	17.6	1.2	0.60	0.32	0.83
Wet	48.7	1.9	1.33	0.61	0.59

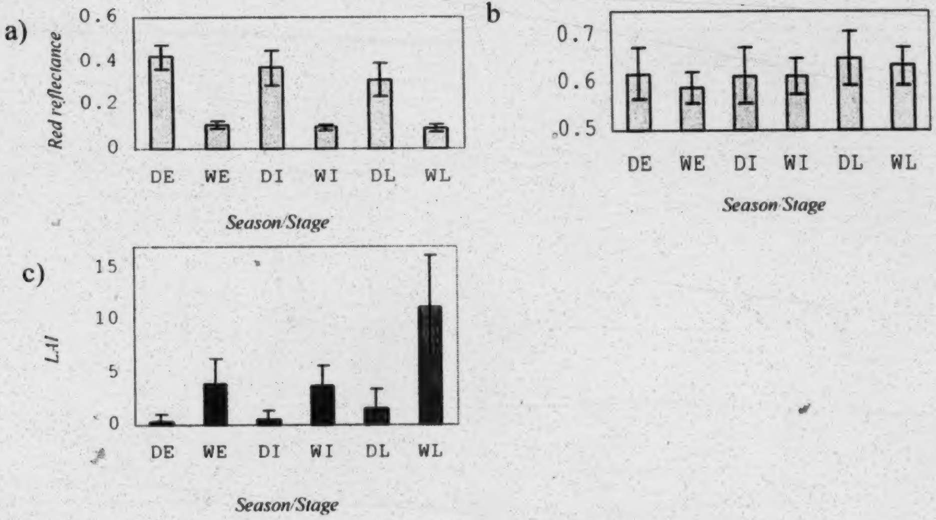

Figure 4.1. Mean and one standard deviation for red (a) and near infrared (NIR) reflectance (b) for the different successional stages per season. Mean and standard deviation for LAI (c) in the different successional stages per season where D = dry season, W = wet season, E = early stage, I = intermediate stage and L = late stage.

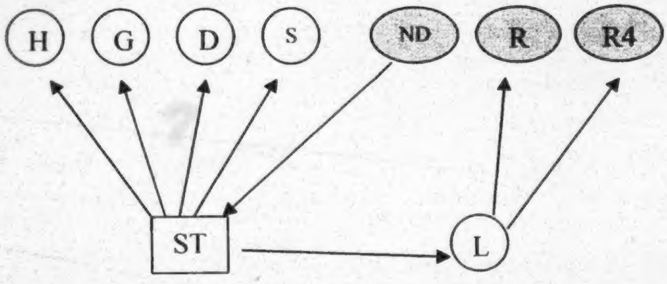

Figure 4.2 Bayesian network for the estimation of LAI from satellite imagery. Circular nodes represent continuous variables, square represents discrete. Shaded nodes are instantiated during inference. H=canopy height, G=basal area, D=stem density, S=species density, ST=successional stage, R3=red reflectance, R4=near infrared reflectance, L = LAI and ND=NDVI

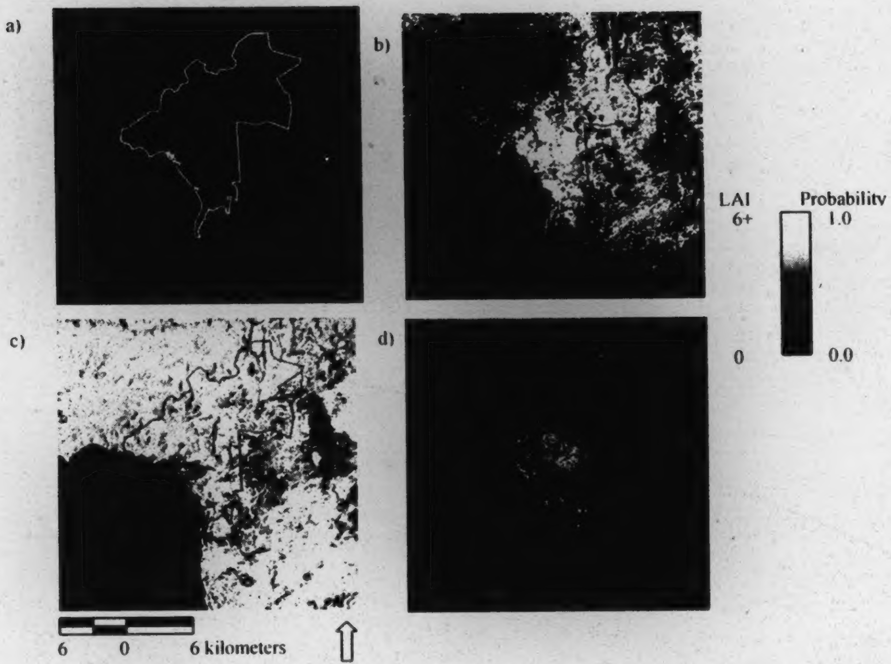
a)
b)
c)
d)
LAI
6+
0
Probability
1.0
0.0
6
0
6 kilometers

Figure 4.3 LAI maps and confidence of LAI prediction maps. a) LAI map of the dry season b) LAI map of the wet season c) confidence of LAI predictions for the dry season and d) confidence of LAI predictions for the wet season. The ocean in the lower left hand corner has been removed from the images. The park boundary is overlain on the images.

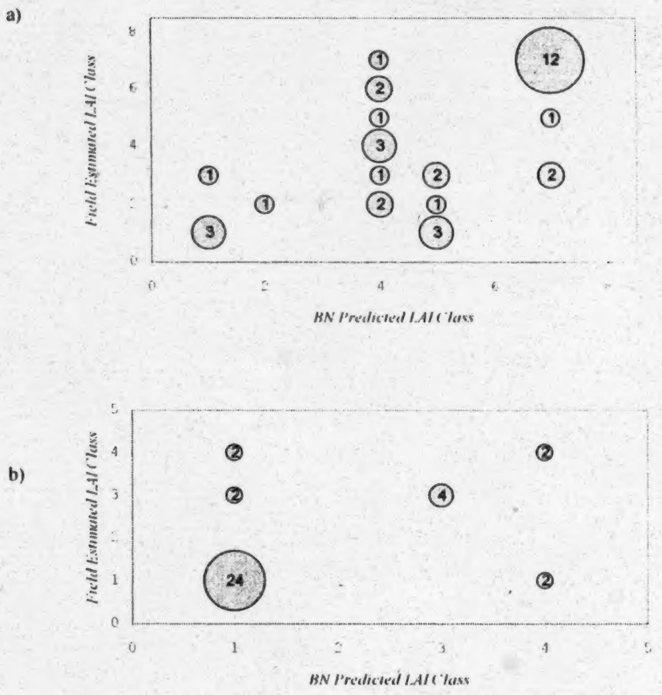

Figure 4.4. Predicted LAI classes from the BN vs. the field estimated LAI classes for a) wet season and b) dry season. The size of the point and the numbers within indicate the number of cases (pixels) represented by each point.

Chapter 5: Effects of seasonal and successional stage on leaf area index and spectral vegetation indices in three Mesoamerican tropical dry forests[1]

5-1. Introduction

Foliage adapts well to temporal changes in the environment, such as changes in illumination or water stress (Welles 1990). In Neotropical dry forest environments foliage is one of the most dynamic components. For most woody species, foliage is the exchange surface between the photosynthetically active component of the vegetation and the atmosphere and controls the light, thermal and hydric conditions within the canopy (Fernandes *et al*. 2003, Fournier *et al*. 2003). Knowledge about the seasonal dynamics of foliage is important for modeling biosphere processes (e.g. water and carbon cycles), which in turn aid in the understanding of biological and physical processes associated with vegetation (Colombo *et al*. 2003).

Leaf area index (LAI) is a simple measure of the amount of foliage and can be estimated relatively rapidly with optical instruments. The formal definition we adopt in this study for LAI is the amount of foliage per unit surface area (projected one sided LAI) (Fournier *et al*. 2003). Optical techniques for estimating LAI are often preferred over allometric or litter trap analyses because these former methods are far more time consuming and labor intensive (Dufrène & Bréda 1995, Maass *et al*. 1995, Leblanc & Chen 2001).

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The interpretation of remotely sensed data (e.g. satellite imagery) offers a tool for rapid assessment of variables such as LAI over large areas and is more economically and logistically viable than intensive field surveys. Maps of biophysical variables produced by remote sensing techniques assist policy makers in creating new conservation areas and biological corridors, and inform biologists or ecologists interested in the state of the habitat of any number of organisms. In other tropical forest locations such as the tropical moist forest, LAI has been shown to have a good relationship with forest structure (Kalacska *et al.* 2004b). This relationship may improve forest classification, and increase understanding of landscape dynamics, forest restoration, impacts on the water and CO_2 exchange. LAI also is related to light transmittance in forests and to averages and variation in understory light, which in turn is important for regeneration. Currently, we have a relatively poor under understanding of LAI in tropical ecosystems and consequently many interesting applications have not been developed using this ecological concept.

Optical instruments such as the LAI-2000 (LI-COR 1992) estimate plant-area-index (PAI) because they cannot discriminate between foliage and the woody component of the canopy. Included in the estimates of PAI are the contributions of the trunks, branches, etc. (Kucharik *et al.* 1998). By applying site-dependent calibration equations, LAI can be calculated from PAI. The LAI-2000 estimates the amount of diffuse radiation below 490 nm that infiltrates the canopy. The instrument is composed of five concentric sensor rings with fields of view centered between 7 ° and 68 °.

Consequently our main objective is to evaluate seasonal PAI/LAI and canopy openness for three sites of tropical dry forest in Mesoamerica. We also explore the role of differences in forest structure on PAI/LAI. Finally, we evaluate regression models to estimate PAI/LAI from spectral vegetation indices calculated from satellite imagery. We address the following questions: Are there significant differences in tropical dry forest structure in different stages of succession among different geographic locations? Are there significant differences in PAI, LAI, and canopy openness between geographic locations, successional stages, and seasons? Are there significant correlations between PAI, LAI and spectral vegetation indices calculated from satellite imagery? Can PAI /LAI be mapped from satellite imagery from the tropical dry forest?

We expect that both structure (an indication of successional stage) and climate will have an effect on LAI/PAI. With an increase in structural complexity during succession (i.e. greater basal area, taller canopy height, etc.) we expect an increase in PAI/LAI. In addition, we expect that a harsher climate with greater restrictive growth forces (i.e. longer dry season, less precipitation, etc.) will have a negative effect on PAI/LAI.

5-2.Methods

5-2.1 Study areas

We studied three geographic locations spanning a climatic gradient from a very dry tropical forest to a moist transitional tropical dry forest. The first and driest site is located in the Chamela Biological station in the Chamela-Cuixmala Biosphere Reserve, state of Jalísco, México (19° 22'N-19° 39'N, 104° 56'W-

105°-10'W). This region has both high species richness (ca 1120 known vascular plants) and high endemism (Lott 1985). The station encompasses 3300 ha and is unique in that the forest has most likely been undisturbed for hundreds of years (Maass & Martinez-Yrizar 2001). We examined three physiognomically different forest types in and around the station: upper ridge-top forest (late succession to relatively undisturbed; L), intermediate (I), a secondary forest, and early (E), the first stage of regeneration populated entirely by low *Acacia* sp. bushes. The vegetation at Chamela is dominated by tropical deciduous forest, with some patches of tropical riparian evergreen forest in the stream beds (Rzedowski 1978). Plants that occur in these habitats differ in their phenology and moisture availability (Lott *et al.* 1987, Balvanera *et al.* 2002). Deciduous habitats are seasonal and xeric, while riparian habitats are aseasonal and mesic. Deciduous and riparian habitats have similar numbers of plant species, but the latter includes a greater number of species of climbers. Some plant species are common and ubiquitous in both habitats (Lott *et al.* 1987). The highly seasonal climate is illustrated in Figure 5.1.

The second site is located in the Santa Rosa National Park (a World Heritage Site), a sector of the Area de Conservación Guanacaste in NW Costa Rica (10° 48'N, 85° 36'W) (Janzen 2000). Santa Rosa is considered as transitional between the tropical dry forest and the tropical moist forest. The yearly precipitation is highly variable (i.e. 915-2258 mm, Janzen 1993), most of which is generally concentrated in generally only six months of the year (Figure 5.1). The uplands of the park are a mixture of secondary forest in different stages of succession with various land use and anthropogenic fire histories (Janzen 1986, 1988a-c, 2000, Arroyo-Mora *et al.* 2005, Kalacska *et al.* 2004a). The area encompassing Santa Rosa and the land around it have endured severe deforestation from multiple socioeconomic pressures such as clearing lands for pasture, agriculture, timber extraction, and most recently tourism (Quesada & Stoner 2004). The vegetation is drought deciduous (Gentry 1995, Lobo *et al.* 2003). We refer to three stages of succession in this study: early (E; many small trees, shrubs and open areas) intermediate (I; heterogeneous canopy, deciduous trees and lianas) and late (L; dominant canopy, shade tolerant species, overlapping crowns) (Arroyo-Mora *et al.* 2005, Kalacska *et al.* 2004a).

The third site is located in the Palo Verde National Park in the Area de Conservación Tempisque in NW Costa Rica (10° 21'N, 85° 21'W). The park is composed of dry deciduous forest along limestone outcrops, savanna, mesic forest, mangrove forest and an extensive seasonal wetland region beside the Tempisque River (Frankie *et al.* 1993). It is both a Ramsar Convention of Wetlands site and one of the areas with the greatest ecological diversity in Costa Rica. This area was a cattle ranch dating back to the 1920s until a portion was expropriated in the 1970s for a new settlement program and later a portion (4800 ha) was declared a wildlife refuge (Quesada & Stoner 2004). Palo Verde National Park (10,000 ha) was officially created in 1981. The protected area was expanded several times and now includes the Lomas Barbudal Biological Reserve and a corridor between reserves for a total area of 20,000 ha (Quesada & Stoner 2004). Cattle have been used in the past in Palo Verde as a means to control fires and manage the wetlands (Mozo 1995) with mixed results; however, currently there is a new management plan in effect and the cattle have been removed. As for Santa Rosa, we refer to the same three stages of forest succession.

For all three sites, even with differences in chronological age and land use history, there are commonalities in the structure between what we describe as "stages." The description of what constitutes a specific stage is unique to each site, but through this approach (as opposed to age), we remove the differences in the types and intensities of past (prior to abandonment) and intermediate (after abandonment) land uses as confounding factors. In addition, as described in Arroyo-Mora *et al.* (2005), the stages have specific reflectance signatures which separate them (i.e. percent crown cover with foliage during the transition season and vegetation indices). The repeatability of the structural approach is that it allows for similar characteristics (both structural and remotely sensed) to be applied elsewhere, in areas with different land-use histories.

5-2.2. Forest Structure

Forest structure was inventoried in 20 x 50 m (0.1 ha) plots in all stages (Table 5.1) for Palo Verde (in March) and Chamela (in August), where the diameter at breast height (DBH) of all living woody stems with a DBH $\geq$ 5 cm was measured. For multi-stemmed individuals each stem with a DBH $\geq$ 5 cm was considered as an individual. The height of the six tallest trees was also measured with a clinometer. Data from Santa Rosa were adapted from a previous study conducted with the same methodology (Kalacska *et al.* 2004a) for a total of 51 0.1 ha structure plots (Figure 5.2 and Table 5.1). In addition, from this structure data we calculated the Holdridge complexity index (C_{HCI}) (Holdridge 1967, Holdridge *et al.* 1971) as modified by Lugo *et al.* (1978) to include stems with a DBH $\geq$ 5 cm:

$$C_{HCI} = \frac{HGDS}{1000} \qquad (1)$$

where H is canopy height (m), G is basal area (m^2/ha) , D is the number of stems and S is species density (number of species per 0.1 ha).

5-2.3 Plant Area Index, Leaf Area Index and Canopy Openness.

Plant area index (PAI) was estimated optically with the LAI-2000 in the dry (March all three sites) and wet (SR: November, PV: July, CH: August) seasons in a subset of 44 plots (30 x 60 m) encompassing the forest structure plots described above (Table 5.1). PAI estimates were acquired in an offset grid sampling scheme to maximize the surface area covered by the measurements without overlap (Kalacska *et al.* 2005). The number of measurements per plot varied from 12 to 100 depending on the height of the canopy. More measurements were necessary in the early stages (because of a lower canopy height) to cover the area of the plot. PAI measurements were taken at a height of approximately 1.5 m from the ground. Subsequently, PAI was converted to LAI for Santa Rosa and Palo Verde with the regression models developed from litter trap data described in Kalacska *et al.* (2005a). These calibration models were developed from leaf litter collected (and dried to constant weight) monthly over one leaf fall cycle. Specific leaf area was then calculated for 63 species (from fresh leaves). Subsequently, LAI was calculated for the leaves in the litter traps on a per species basis using the specific leaf area. The optical estimates of PAI (collected at the same time as the leaf litter) were then calibrated with regression models between the optical estimates and the litter traps (see Kalacska *et al.* 2005a for complete details). For Chamela, calibration equations were not available for the LAI-2000 and therefore, for this site we refer to PAI throughout the analyses and compare results from Chamela only with PAI for Palo Verde and Santa Rosa.

Canopy openness was estimated for all three sites from hemispherical photographs (Nikon CoolPix 995) in the dry (March for all sites) and wet seasons (SR: November, PV: July, CH: August) with 10 photographs per plot taken at 1.5 m camera height. The photographs were processed with Gap Light Analyzer v. 2.0 (SFU-IES 1999). This program extracts canopy structure information (i.e. gap fraction, canopy openness, effective LAI, etc.) from hemispherical photographs (SFU-IES 1999). In addition, we calculated wood-area-index (WAI), the contribution of the woody component (i.e. branches, trunks) to PAI, with the same program using the photographs from the dry season.

5-2.4 Satellite image processing and vegetation index calculations.

The satellite images used in this study were multi-spectral images from Landsat 7 ETM+ (28.5 m spatial resolution) acquired in the wet (SR: November, PV: November, CH: August) and dry (SR: April, PV: April, CH: March) seasons for each site. The digital numbers from the images were converted to surface reflectance with the ATCOR v.2.0 module for ERDAS Imagine v.8.6 using standard estimates for a tropical rural atmosphere. We use surface reflectance rather than digital numbers or radiance because studies have shown that surface reflectance is the most sensitive to canopy structural properties (Huete *et al.*

1997). The pixels values for each plot were extracted from the images in a 3x3 pixel window (0.7 ha) around the centre of each plot. The coefficient of variation in these windows was generally less than 10 percent.

From the reflectance values for each image we calculated four spectral vegetation indices (SVIs) from the red and near infra-red bands: Simple ratio (SR), normalized difference vegetation index (NDVI) (Rouse *et al.* 1974), soil adjusted vegetation index 2 (SAVI2) (Qi *et al.* 1994) and modified single ratio (MSR) (Chen 1996).

$$SR = \frac{\rho_n}{\rho_r} \tag{2}$$

$$NDVI = \frac{\rho_n - \rho_r}{\rho_n + \rho_r} \tag{3}$$

$$SAVI2 = \rho_n + 0.5 - \sqrt{(\rho_n + 0.5)^2 - 2 \times (\rho_n - \rho_r)} \tag{4}$$

$$MSR = \frac{\frac{\rho_n}{\rho_r} - 1}{\sqrt{\frac{\rho_n}{\rho_r} + 1}} \tag{5}$$

Other studies have highlighted the utility of the mid infrared bands (i.e. band 5 and 7) for vegetation phenology, moisture and total stand biomass (Knipling 1970, Bohlman *et al.* 1998, McMorrow 2001). However, it has been shown that in the same study area as our study, indices using these bands are not sensitive to changes in canopy structure (Arroyo *et al.* 2005). We have therefore limited the scope of this analysis to the red and near infrared bands.

5-2.5 Analyses

We examined differences in forest structure, PAI, LAI, and canopy openness between sites and between successional stages within the sites using non-parametric Mann—Whitney and Kruskal—Wallis tests. To infer which canopy characteristics have the greatest influence on PAI, we performed a multiple least-squares regression with forest structure variables and canopy openness. Subsequently, we examined a number of nonlinear transition functions to infer PAI/LAI from the satellite images. In general, in the remote sensing literature, nonlinear regression has not been as popular as linear regression. Nonlinear functions however, such as transition functions can describe the relationship between variables such as spectral vegetation indices and LAI or PAI. They can also provide insights (i.e. the range of sensitivity without saturation) into the relationships between the variables that cannot be determined as easily from linear models (Kalacska *et al.* 2004b). To conclude the analysis we created LAI/PAI maps for the three study sites using the best fit regression equations.

5-3. Results

5-3.1 Tropical Dry Forest Structure

We illustrate the results for canopy structure in Table 5.2. For the early stage, because the vegetation in Chamela was comprised of a monospecific stand of *Acacia* sp. bushes where all the stems were below 5 cm in diameter, we included only Palo Verde and Santa Rosa for the statistical analysis. We found a significantly higher stem density (No. of stems) (Mann—Whitney U=4.0, P = 0.014) and species density (Mann—Whitney U = 6.5, P = 0.034) in Santa Rosa than Palo Verde. For the intermediate stage we included all three sites and found significant differences with a Kruskal—Walls test for each structural variable and the Holdridge complexity index with the exception of stem density (height: H = 6.5, *P* = 0.039, basal area: H = 11.4, *P* = 0.003, species density: H = 14.9, *P* = 0.001, Holdridge complexity index: H =7.4, *P* = 0.025). The greatest average tree height and basal area were in Palo Verde whereas the highest number of species and Holdridge complexity index was in Santa Rosa.

For the late stage, we also included the three sites. We found significant differences in all structural variables and the Holdridge complexity index with the exception of species density (height: H = 9.4, *P* = 0.009, basal area: H = 7.7, *P* = 0.021, stem density: H =8.2, *P* = 0.016 and Holdridge complexity index: H = 10, *P* = 0.007). The greatest canopy height was found in Palo Verde, the highest basal area and Holdridge complexity index in Santa Rosa and the highest number of stems in Chamela.

5-3.2 Plant Area Index, Leaf Area Index and Canopy Openness

At the regional level, in the wet season we found differences in PAI at all stages (early: U = 5.5, *P* = 0.03, intermediate: H = 9.5; *P* = 0.01; late: H = 9.0, *P* = 0.01). The highest PAI was found in Santa Rosa in all stages. In the dry season PAI was greater in the early stage at Santa Rosa than the early stage in Palo Verde (U=6.0, *P*=0.03). This finding was corroborated with the values of canopy openness: 70 percent in Santa Rosa, 85 percent in Palo Verde. For these analyses the early stage was not included from Chamela because the majority of the *Acacia* sp. bushes were below the height of the LAI-2000 sensor. We did not find a difference in the intermediate or late stages in PAI in the dry season between the sites.

In terms of canopy openness, in the wet season we only found a difference between the early stage in Palo Verde (75 percent canopy openness) and Santa Rosa (31% canopy openness) (U = 37.0, $P = 0.02$). We did not find differences between canopy openness for the intermediate and late stages for the three sites (wet season). In the dry season, again we found a difference in canopy openness only between the early stages of Palo Verde (85 %) and Santa Rosa (70 %). For LAI (data only for Palo Verde and Santa Rosa), we found a significant difference only in the wet season between the early (U = 4.0, $P = 0.01$) and intermediate stages (U = 9.0; $P = 0.04$); the two sites with Santa Rosa being the highest. For Palo Verde and Chamela, there was a strong negative correlation between PAI and canopy openness for both seasons (stronger than -0.90; Table 5.3). For Santa Rosa, the correlation was also negative, but only -0.61 in the dry season and -0.79 in the wet season. All three sites exhibited a decreasing exponential relationship between canopy openness (CO) and PAI in the wet season and a linear relationship in the dry season (Figure 5.3). The regression equations are listed in Table 5.3. PAI in the dry season (WAI) vs PAI from the wet season showed a slight positive trend (data not shown) for all three sites.

We observed a slight positive relationship between the complexity index and PAI for both seasons (Figure 5.4). There was no relationship between canopy openness and the complexity index in the dry season and a slight decreasing trend in the wet season (Figure 5.4).

The most influential canopy characteristics on PAI are listed in Table 5.4. In the wet season, the predominantly influential characteristic is canopy height. In Santa Rosa, as stem density, and height increased and dry season canopy openness (indication of amount of woody matter) decreased, PAI increased. In Chamela in the wet season, height and wet season canopy openness were inversely related with PAI, whereas basal area was positively related. In the dry season the most influential characteristic on PAI for all sites was dry season canopy openness (Table 5.4). In all cases, as canopy openness from the dry season decreased, PAI increased.

At the stage level, for all three sites canopy openness decreased with increasing successional stage in both seasons (Figure 5.5a). PAI however, increased with increasing successional stage (Figure 5.5b). With calibration data only available for the Costa Rican sites, we compared LAI only between Palo Verde and Santa Rosa (Figure 5.5c). During the dry season, there was no difference between the early and intermediate sites in either location. During the wet season in Santa Rosa, there was no difference between the early and intermediate stages. From the hemispherical photos, WAI in Palo Verde was calculated to be 0.27 ± 0.1 for the early stage, 0.73 ± 0.5 for the intermediate stage and 0.80 ± 0.2 for the late stage. In Chamela WAI was calculated as 0.12 ± 0.05 for the early stage, 0.56 ± 0.3 for the intermediate stage and 0.79 ± 0.18 for the late stage. From Kalacska *et al.* (2005a) WAI was 0.4 ± 0.27 for the early stage, 1.07 ± 0.43 for the intermediate stage and 0.4 ± 0.14 for the late stage in Santa Rosa.

5-3.3 Red and near-infrared reflectance

A decreasing trend in red reflectance (band 3) was seen from the early to the late stages in Palo Verde (25-13 %) and Santa Rosa (27-18 %) in the dry season (Table 5.5). In Chamela however, red reflectance decreased from the early (12 %) to the intermediate (9 %) but increases to the late (11%). Near infrared reflectance (band 4) increased from the early to the late stage in Palo Verde (16-20 %) and Santa Rosa (40-43 %) in the dry season. The opposite trend was seen in Chamela with the near infrared reflectance decreasing from the early to the late stages (27-16 %).

In the wet season, red reflectance decreased from the early to the late stages in Palo Verde (22-16 %) (Table 5.5). There was a slight 1 percent decrease in Santa Rosa for the same stages. In Chamela there was no difference between the early and late stages (16 %) but a slight 3 percent increase in the intermediate stage. An increase in near infrared reflectance could be seen through the stages for Palo Verde (50-56 %) and Santa Rosa (37-41%). In Chamela near infrared reflectance increased slightly from the intermediate stage (43 %) to the late stage (44 %) but the early stage had the highest reflectance in the near infrared at 45 percent.

5-3.4 Non-linear Regression Analyses

After considering several transition functions, we found that the Lorentzian Cumulative function best described the relationship between the spectral vegetation indices and LAI/PAI (Table 5.6) for the wet season. The Lorentzian Cumulative function has the following form:

$$y = \frac{a}{\pi}\left(\arctan\left(\frac{x-b}{c}\right) + \frac{\pi}{2}\right) \qquad (6)$$

where a = the transition height, b = the transition midpoint and c = the half-width of the transition. The transition height is the range of the SVI values which are sensitive to changes in LAI. The transition center is the LAI value at the midpoint of the transition and the half-width of the transition is half of the range of LAI values to which the SVI is sensitive to. Of the four SVIs calculated for each site, the SVI with the best relationship to LAI (Palo Verde and Santa Rosa) or PAI (Chamela) is illustrated in Table 5.6.

Because not all the parameters (a-c) were statistically significant, we cannot comment on the range of the sensitivity of the indices (a larger range of values is necessary). By inverting the function however, we created LAI/PAI maps of the study areas in the wet season (Figure 5.6):

$$LAI = b - cTan\left(\frac{\pi(a - 2\times SVI)}{2a}\right) \qquad (7)$$

where the constants (a-c) are the same as described above.

5-4. Discussion

Across sites, the extent and harshness of the dry season (Figure 5.1) influenced the overall canopy structural components (i.e. more restrictive growth factors). For example, in Chamela, with the longest dry season, the Holdridge complexity index was consistently lower than either of the other two sites for all stages (Table 5.2). In the late and intermediate stages, canopy height and basal area were also lowest in Chamela in comparison to the Costa Rican sites while in contrast, stem and species densities were the highest (Table 5.2). For the early stage, the composition and structure was much simpler (i.e. monospecific stand of *Acacia* sp. bushes) that either Costa Rican site, both of which had a representation of individuals with a DBH ≥ 5cm.

In the dry season, regardless of the differences in forest structure, the LAI-2000 perceived the same woody canopy structure in all sites in the late stage (i.e. no difference in PAI or canopy openness). In the wet season, horizontally (for example as seen from below looking up) the canopies (from the late stage) did not differ between the three sites (i.e. no difference in CO). PAI however, was different. This indicates that it is the vertical component of the canopy (i.e. additional layers of foliage) which was different between the sites. This was supported by the negative correlation between PAI and height in Chamela, as opposed to a positive correlation for the sites in Costa Rica. For example, the woody component of the vegetation in this stage was much denser (i.e. more lianas, more stems) in Chamela than for the sites in Costa Rica. With a shorter canopy this density was accentuated (i.e. more woody matter in a smaller vertical space) and therefore, PAI increased.

In the early stage in Chamela in the dry season, the largest contributor to reflectance was bare soil followed by dry woody matter. In Palo Verde, dry grass (e.g. *Hyparhennia rufa* (L.)) was the predominant contributor to reflectance followed by woody matter (i.e. bark). In Santa Rosa there was a broader range in the dominant contributor to reflectance because of the range of canopy types (i.e. very sparse trees to a heterogeneous but relatively continuous canopy). In the wet season, in Chamela the reflectance from the early stage was predominantly from a thick inhibitory grass, shrub and herb layer (high green biomass). In Palo Verde a similar grass and shrub layer was seen with sparse trees in full foliage while in Santa Rosa the tree canopy had a greater influence on reflectance (indicative of the more developed canopy). In all three sites in the intermediate and late stages there was an increase in green biomass as the forest matured. The dominance of the reflectance in the wet season by a thick inhibitory grass layer in the pastures/open areas has been noted by Kalacska et al. (2005b) for Santa Rosa where the reflectance of the *H. rufa* in the open pastures approximated that of the early and in some case the intermediate successional stage and impeded the estimation of LAI from the imagery.

With regard to the relationship between PAI and forest structure, throughout the three study areas, sites with low PAI in both seasons were mostly open, without a developed tree canopy. Sites with a large difference between the dry season PAI and the wet season PAI were areas with a well-developed canopy (multistratal) with a large turnover in foliage between the seasons. Sites with a high PAI in the dry season and relatively small differences in PAI in the wet season were indicative of areas with a large woody component (e.g. many woody lianas) whereas areas with a low PAI in the dry season and a high PAI in the wet season had a thicker seasonal understory which was tall enough to be part of the

PAI estimates in the wet season. An increase in the woody component and foliage (PAI) with increasing forest structure was also apparent. However, the same trend was not seen with canopy openness because it is more a measure of the horizontal structure and an increase in forest structure (C_{HCI}) is indicative of development as seen in both planes. In addition, the results from the inter site and intra site comparisons of PAI/LAI indicated that degree of deciduousness is not species composition, or stage dependent. Rather, the topographic and climatic conditions influence the degree of deciduousness. For example, all stages in Chamela were nearly 90% deciduous, however, in Santa Rosa and Palo Verde, degree of deciduousness decreased with increasing successional stage (species composition data not shown). In addition, in the area with the greatest degree of deciduousness, Chamela, there is a large representation of cacti, agaves, and bromeliads (Gentry 1995). In the Costa Rican sites PAI increased with an increasing height and structure. At shorter canopy heights in the Costa Rican sites the forest was more open with mostly saplings and small trees; therefore, as the height decreased the vegetation was more open rather than denser (as is seen in Chamela).

By mapping LAI/PAI in the wet season we captured full foliage rather than density of the woody component. The different classes are clearly distinguishable visually on the classified LAI/PAI maps. The utility of these maps is providing an overview not only of the LAI/PAI but also a tool for interpreting the suitability of the forest as a habitat for various types of fauna or flora. For example, forest areas with higher LAI, such as riparian corridors in the dry season, may be suitable locations for the foraging territories of *Noctilio* sp. bats. Also, using the LAI maps, patches of forest that are potentially suitable habitat types for species such at the Mexican Long Nosed Bat (*Leptonycteris nivalis)* or the Great False Vampire Bat (*Vampyrum spectrum)* can be found. Or for example, areas identified as old successional forests may provide and indication of areas that are among the last few patches containing mature individuals of trees such as the *Guaiacum sanctum* (Ironwood), an extremely rare, slow growing, and valuable timber species. Further development of the maps would include a comprehensive spatial error assessment to validate the estimations of LAI/PAI and to identify problems areas that require a more detailed analysis to refine the estimations.

5-5. Conclusions

We attribute the majority of the differences in structure, canopy openness and PAI/LAI between the three sites to both climate and differences in land use and land management practices. The late stage in Chamela was the only area which has not been anthropogenically disturbed in hundreds of years. The longer and harsher dry season however, slows the development of the disturbed areas. In Palo Verde the most intense land use has been the management practices with cattle. Stern *et al*. (2004) have shown that these areas had a different structure and composition as those that had been minimally affected by cattle. In Santa Rosa, the landscape was a mosaic of various previous land uses such as cattle ranching, agriculture, inland rice, etc., as well as different frequencies of anthropogenic fire

(Kalacska *et al.* 2004a). We believe these differences were also manifested in the observed values of PAI and LAI.

In the future, calibration functions need to be developed for the LAI-2000 in Chamela in order for a more thorough comparison between the sites. Other forest types such as Riparian and mangrove forests should also be included in the analyses. In addition, hyperspectral remotely sensed data such as Hyperion and HyMap should be investigated in order to produce more detailed maps of LAI. The effect of soil types, nutrient content and soil properties (e.g. water holding capacity) should also be examined as other potential factors influencing the forest structure and PAI/LAI.

From our current analyses, using spectral vegetation indices to infer LAI/PAI, we found that a Lorentzian Cumulative function best described the relationship between the indices and LAI/PAI. For Chamela and Palo Verde the modified simple ratio (MSR) had the strongest relationship with LAI/PAI. In Santa Rosa the soil adjusted vegetation index 2 (SAVI2) had the best relationship.

In this study we have highlighted the different structural elements of the canopy that influence PAI/LAI. Taking these into consideration in addition to climatic effects at various locations will result in more precise representations of this key variable at the regional level. For quantifying environmental services and sustainable development practices, a better understanding of the physical forest characteristics and how they are interdependent is required. This study has shown regional differences in PAI/LAI and illustrated the possibility for mapping these variables from remotely sensed imagery for use in conservation policy development, environmental services or other studies requiring such data.

5-6. References

ARROYO-MORA, J. P., G.A. SANCHEZ-AZOFEIFA, M. KALACSKA B. RIVARD, J.C. CALVO-ALVARADO, AND D.H. JANZEN. 2005. Secondary forest detection in Neotropical dry forest using Landsat 7 ETM+ imagery. Biotropica 37: xxx-xxx.

BALVANERA P., LOTT E., SEGURA G., SIEBE C. AND A. ISLAS. 2002. Patterns of β diversity in a Mexican tropical dry forest. J.Veg. Sci. 13: 145-158.

BOHLMAN, S., J. B. ADAMS, M. O. SMITH, AND D. L. PETERSON. 1998. Seasonal foliage changes in the Eastern Amazon Basin detected from Landsat Thematic Mapper Satellite Images. Biotropica. 30: 376-391

BROWN S. AND A.E. LUGO. 1982. Storage and production of organic matter in tropical forests and their role in the global carbon cycle. Biotropica 14: 161-187.

BURNHAM R. J., 1997. Stand characteristics and leaf litter composition of a dry forest hectare in Santa Rosa National Park, Costa Rica. Biotropica 29: 387-395.

CHEN J. M. 1996. Evaluation of vegetation indices and a modified simple ratio for Boreal applications. Can. J. Remote Sens.22: 229-241.

COLOMBO R., BELLINGERI D., FASOLINI D., AND C. M. MARINO. 2003. Retrieval of leaf area index in different vegetation types using high resolution satellite data. Remote Sens. Env. 86: 120-131.

DUFRÈNE E. AND N. BRÉDA. 1995. Estimation of deciduous LAI using direct and indirect methods. Oecologia, 104: 156-162.

ESTADO DE LA NACION EN DESARROLLO HUMANO SOSTENIBLE. 1997. Un analisis amplio y objetivo sobre la Costa Rica que tenemos a partir de los indicators mas actuales (1998). 1st ed. 37pp.San Jose: Editorama S.A.

FERNANDES R. F., F. BUTSON, S.G. LEBLANC, AND R. LATIFOVIC. 2003. Landsat-5 TM and Landsat 7 ETM+ based accuracy assessment of leaf area index products for Canada derived from SPOT-4 VEGETATION data. Can. J. Remote Sens. 29: 241-258.

FOURNIER R. A., D. MAILLY, J.-M.WALTER, AND K. SOUDANI. 2003. Indirect measurement of rest canopy structure from in situ optical sensors. In: Wulder M., Franklin S. (Eds). Methods for remote sensing of forests: concepts and case studies. pp.77-114. Kluwer Academic Press.

FRANKIE G.W., L. NEWSTROM, S.B. VINSON, AND J.F. BARTHELL. 1993. Nesting-habitat preferences of selected *Centris* bee species in Costa Rican dry forest. Biotropica 25: 322-333.

GENTRY A. H.1995. Diveristy and floristic composition of neotropical dry forests. In: Mooney, H.A., Bullock S.H., Medina E. (Eds), Seasonally dry tropical forests., pp. 146-194 Cambridge University Press, Cambridge.

HOLDRIDGE L. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica. 206pp.

HOLDRIDGE L., Renke W.C., Hatheway W. H., Liang T. AND Tosi Jr., J. 1971. Forest environments in tropical life zones: A pilot study, Pergamon Press, New York. 747pp.

HUETE, A. R., H.Q. LIU, K. BATCHILY, AND W. VAN LEEUWEN. 1997. A comparison of vegetation indices over a global set of TM images for MODIS-EOS. Remote Sens. Environ. 59: 440-451.

JANZEN, D. H. 1973. Tropical agroecosystems. Science 182: 1212-1219.

_______. 1983. Costa Rican Natural History. University of Chicago Press, Chicago. 816pp.

_______. 1986. Tropical dry forests: the most endangered major tropical ecosystem. In: Wilson, E.O. (Ed)., Biodiversity, pp. 130-137. National Academy Press, Washington, D.C.

_______. 1988a. Guanacaste National Park: Tropical, Ecological and biocultural restoration. In: Carins, J.J. (Ed), Rehabilitating damaged ecosystems, vol. II. pp. 143-192. CRC Press, Boca Raton, FL..

_______. 1988b. Management of habitat fragments in a tropical dry forest: Growth. Annals of the Missouri Botanical Garden, 75: 105-116.

_______. 1988c. Complexity is in the eye of the beholder In: Almeda F., Pringle C.M. (Eds), Tropical rainforests: diversity and conservation, pp. 29-51. California Academy of Science and AAAS, San Francisco.

______.1993. Caterpillar seasonality in a Costa Rican dry forest. In: Stamp N.E., Casey T.M. (Eds) Caterpillars: Ecological, Evolutionary Constraints on Foraging. pp.448-477. Chapman and Hall, New York.

______. 2000. Costa Rica's Area de Conservación Guanacaste: a long march to survival through non-damaging biodevelopment. Biodiversity 1: 7-20.

KALACSKA M., J.C. CALVO-ALVARADO, G.A. SANCHEZ-AZOFEIFA. 2005a. Calibration and assessment of seasonal changes in leaf area index of a tropical dry forest in different stages of succession. Tree Physiol. 25: 733-744.

KALACSKA M., G. A. SANCHEZ-AZOFEIFA, T. CAELLI, B. RIVARD, B. BOERLAGE. 2005b. Estimating leaf area index from satellite imagery using Bayesian Networks. IEEE T. Geosci. Remote. In press.

KALACSKA M., G.A. SANCHEZ-AZOFEIFA, J.C. CALVO-ALVARADO, M. QUESADA, B. RIVARD, D.H. JANZEN. 2004a. Species composition, similarity and diversity in three successional stages of a seasonally dry tropical forest. Forest Ecol. Manag. 200: 227-247.

KALACSKA M., G.A. SANCHEZ-AZOFEIFA, B. RIVARD, J.C. CALVO-ALVARADO, A.R.P. JOURNET, J.P. ARROYO-MORA, AND D. ORTIZ-ORTIZ. 2004b. Leaf area index measurements in a tropical moist forest: A case study from Costa Rica. Remote Sens. Environ. 90: 134-152.

Knipling E. B. 1970. Physical and physiological basis for the reflectance of visible and near infrared radiation from vegetation. Remote Sens. Environ. 1: 155-159.

Kucharik C. J., J.M. Norman, and S.T.Gower. 1998. Measurements of branch and adjusting leaf area index indirect measurements. Agr. Forest Meteorol. 91: 69-88.

Leblanc S. G. and J.M.Chen. 2001. A practical scheme for correcting multiple scattering effects on optical LAI measurements. Agr. Forest Meteorol. 110: 125-139.

LI-COR Inc. 1992. P[illegible]t Canopy Analyzer Instruction/Operating Manual. LI-COR Inc., Li[illegible]oln NE.

Lobo J. A., M. Quesada, K.E. Stoner, E.J. Fuchs, Y. Herrerias-Diego, J. Rojas-Sandoval, and G. Saborio-Rodriguez. 2003. Factors affecting phenological patterns of Bombacaceous trees in seasonal forests in Costa Rica and Mexico. Am. J. Bot. 90: 1054-1063.

Lott E. 1985. Listados florísticos de México III. La Estación de Biología Chamela, Jalísco, Instituto de Biología, Universidad Nacional Autónoma de México, México.

Lott E. J., S.H. Bullock, AND J.A. Solís-Magallanes. 1987. Floristic diversity and structure of a tropical deciduous forest of coastal Jalísco. Biotropica 19: 228-235.

Lugo A. E., J.A. Gonzalez-Liboy, B. Cintron, and K. Dugger. 1978. Structure, productivity and transpiration of a subtropical dry forest in Puerto Rico. Biotropica 10: 278-291.

Maass J. M., J.M. Vose, W.T. Swank, and A. Martinez-Yrizar. 1995. Seasonal changes in leaf area index (LAI) in a tropical deciduous forest in west Mexico. Forest Ecol. Manag. 74: 171-180.

Maass, M., and A. Martinez-Yrizar. 2001. NPP Tropical Forest: Chamela, Mexico, 1982-1995. Data set. Available on-line [http://www.daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A.

McMorrow J. 2001. Linear regression modeling for the estimation of oil palm age from Landsat TM. Int. J. Remote Sens. 22: 2243-2264.

Mozo E. T. 1995. Pastoreo con Ganado vacuno, una alternative del ACT para prevención de incendios forestales, recuperación de humedales y restaruración del bosque tropical seco. Bagaces, Costa Rica: Convenio MIRENEM-Opción Colombia, Universidad Sergio Arboleda. 66pp.

Murphy P. G. and A.E. Lugo. 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. Biotropica 18: 89-96.

______, 1995. Dry forests of Central America and the Caribbean. In: Mooney, H.A., Bullock S.H., Medina E. (Eds), Seasonally dry tropical forests., pp. 9-34. Cambridge University Press, Cambridge.

Quesada M., and K.E. Stoner. 2004. Threats to the conservation of tropical dry forest in Costa Rica. In: Frankie G.W., Mata A., Vinson S.B. (Eds).Biodiveristy in Costa Rica: Learning the lessons in a seasonally dry forest. pp.266-280.University of California Press, Los Angeles.

QI J., Y.H. KERR, M.S. MORAN, M. WELTZ, A.R. HUETE, AND S. SOROOSHIAN. 1994. A soil modified adjusted vegetation index. Remote Sens. Environ. 48: 118-126.

ROUSE J. W., R.H. HAASS, J.A. SHELL, AND D.W. DEERING. 1974. Monitoring vegetation systems in the Great Plains with ERTS-1. Third Earth Resources Technology Satellite Symposium. NASA: Washington DC. pp.309-317.

RZEDOWSKI J. 1978. Vegetación de México. Editorial Limusa, México.

SFU – IES. 1999. Gap Light Analyzer v. 2.0. Available online at: http://www.rem.sfu.ca/forestry/downloads/gap_light_analyzer.htm

STERN M., M. QUESADA, AND K. E. STONER.2002. Changes in composition and structure of a tropical dry forest following intermittent cattle grazing. Rev. Biol. Trop. 50: 1021-1034.

WELLES J. M. 1990. Some indirect methods of estimating canopy structure. Remote Sens. Rev. 5: 31-43.

Table 5.1. Number of plots established for forest structure assessment and Plant Area Index (PAI) estimations

Stage	Palo Verde (structure)	Palo Verde (PAI)	Santa Rosa (structure)	Santa Rosa (PAI)	Chamela (structure)	Chamela (PAI)	Total (structure)	Total (PAI)
Early	6	6	10	7	2	2	*18*	*15*
Inter.	6	6	10	6	4	4	*20*	*16*
Late	3	3	6	3	4	4	*13*	*10*

*Size of structure plots = 20 x 50m, size of PAI plots = 30 x 60m.

Table 5.2 Canopy structure characteristics (including all woody stems DBH ≥5cm) for Chamela Mexico, Palo Verde Costa Rica and Santa Rosa Costa Rica. E = early successional stage, I = intermediate successional stage, L = late successional stage, NC = not cleared. Approximate ages are provided as descriptors of the sites only.

Location – Stage	Height	Basal area	Stem density	Species density	C_{HCI}	Approximate age range
Chamela – E	1.5 ± 0.5	0.0 ± 0.0	0 ± 0	1 ± 0	0.0 ± 0.0	< 5 yrs
Palo Verde – E	7.2 ± 0.8	28.2 ± 18.5	79 ± 25	7 ± 4	17.3 ± 21.8	10 – 30 yrs
Santa Rosa – E	7.5 ± 2.2	11.7 ± 5.4	112 ± 64	15 ± 7	28.0 ± 36.0	0 – 25 yrs
Chamela – I	11.0 ± 2.4	10.4 ± 4.7	146 ± 104	8 ± 6	15.0 ±14.4	15 - 20 yrs
Palo Verde – I	15 ± 2.2	35.7 ± 11.8	78 ± 24	14 ± 3	59.0 ± 29.4	10 – 30 yrs
Santa Rosa – I	10.3 ± 3.4	21.4 ± 6.8	130 ± 35	29 ± 5	68.6 ± 57.7	15yrs – NC
Chamela – L	9 ± 2.2	13.2 ± 2.5	181 ± 4.8	31 ± 12	64.5 ± 24.5	NC
Palo Verde – L	18.3 ± 1.5	29.2 ± 8.1	64 ± 12	19 ± 7	74.8 ± 52.2	NC
Santa Rosa - L	15.0 ± 2.2	30.1 ± 6.5	107 ± 42	29 ± 7	159.0 ± 57.7	15yrs. - NC

Table 5.3. Regression equations and correlation analyses between PAI and canopy openness for the dry and wet seasons for the three study sites. Correlation coefficients are shown in italics.

Location	Dry Season	Wet Season
Palo Verde	PAI = -0.019(CO)+1.8465 R^2=0.96; *-0.98*	PAI = 47.59$(CO)^{-0.9721}$ R^2=0.88; -*0.92*
Chamela	PAI = -0.0217(CO)+1.7475 R^2=0.95; -*0.97*	PAI = 12.716$(CO)^{-0.6679}$ R^2=0.98; -*0.97*
Santa Rosa	PAI = -0.0244(CO)+2.558 R^2=0.35; *-0.61*	PAI = 53.929$(CO)^{-0.949}$ R^2=0.61; -*0.79*

Table 5.4. Most influential canopy characteristics on plant-area-index (PAI) in the dry and wet seasons in order of greatest influence for Chamela Mexico, Palo Verde Costa Rica and Santa Rosa Costa Rica. H = canopy height, G = basal area, D = stem density, COw = canopy openness in the wet season, $\mathrm{CO_d}$ = canopy openness in the dry season. Italics indicate inverse relationship. Same sample size as indicated in Table 5.1. All are statistically significant at the 95% level.

Location	Season	Influential factors	Multiple R^2
Chamela	Wet	*H.* G, *CO_w*	0.99
Palo Verde	Wet	H, *CO_w*	0.91
Santa Rosa	Wet	H, D, *CO_d*	0.92
Chamela	Dry	*CO_d*	0.94
Palo Verde	Dry	*CO_d*	0.96
Santa Rosa	Dry	*CO_d*	0.37

Table 5.5 Red and Near infrared (NIR) reflectance for the dry and wet seasons in the different stages in Chamela, Palo Verde and Santa Rosa

Location-Stage	Red reflectance (%) dry season	NIR reflectance (%) dry season	Red reflectance (%) wet season	NIR reflectance (%) wet season
CH – E	11.9±6.3	26.7±2.5	15.9±2.5	45.1±2.0
CH – I	8.9±4.4	22.4±4.1	19.0±5.8	42.9±19.0
CH – L	11.4±1.5	16.5±1.9	15.6±2.0	44.1±2.2
PV – E	24.8±3.6	15.8±1.8	22.4±2.0	50.0±3.2
PV – I	16.5±4.3	18.3±2.8	17.6±2.2	53.9±4.0
PV – L	12.7±4.7	19.6±4.2	15.7±2.4	56.0±5.6
SR – E	27.0±4.0	40.4±3.6	7.1±1.0	37.3±1.8
SR – I	23.8±5.5	39.5±3.4	6.6±1.0	39.0±3.0
SR – L	18.0±3.4	43.1±5.1	6.0±0.5	41.1±2.9

Table 5.6. Best fit non linear models between LAI /PAI and vegetation indices calculated from the Landsat 7 ETM+ images.

Location	Model	Vegetation Index	Adjusted R^2	P>F	Sites excluded
Chamela[a]	Lorentzian Cumulative	MSR	0.87	<0.000	0
Palo Verde	Lorentzian Cumulative	MSR	0.76	<0.000	0
Santa Rosa	Lorentzian Cumulative	SAVI2	0.71	0.001	2

[a]Values for Chamela are PAI

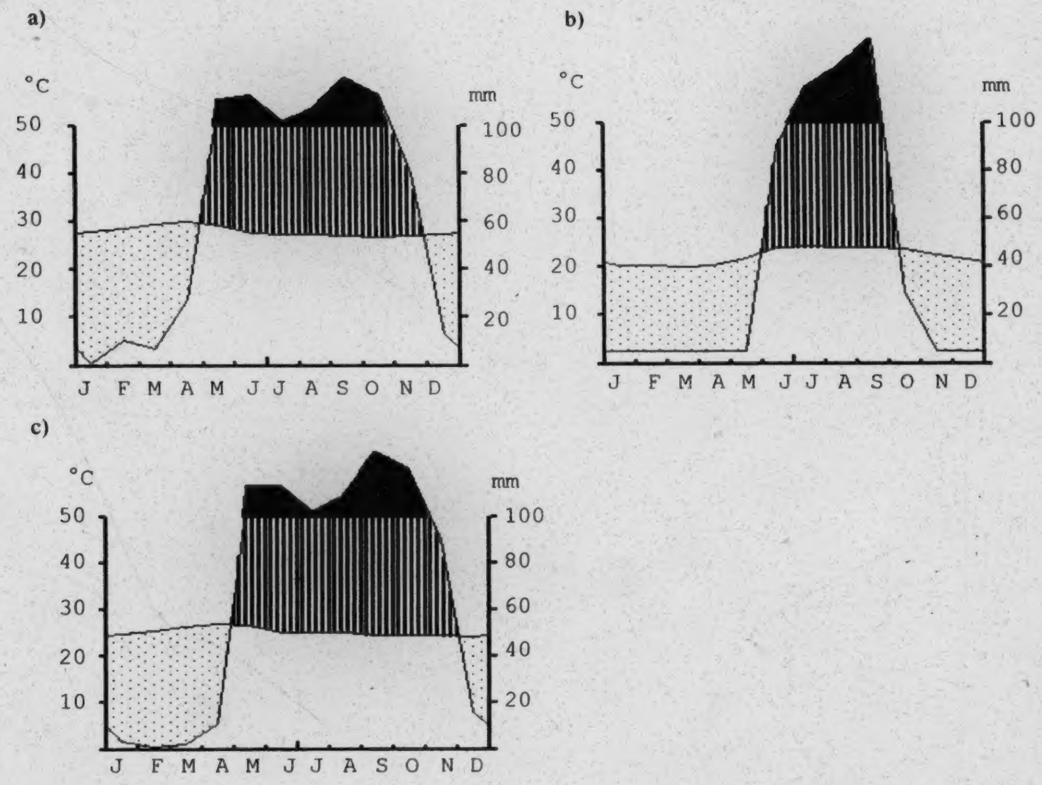

Figure 5. 1 Climate diagrams for Palo Verde Costa Rica (a), Chamela Mexico (b), and Santa Rosa Costa Rica (c). The mean monthly temperature and the monthly precipitation are scaled to represent the potential evapotranspiration. Dry months are represented by the dotted areas, humid months by the vertical lines and wet months (precipitation in excess of 100mm) are in solid black.

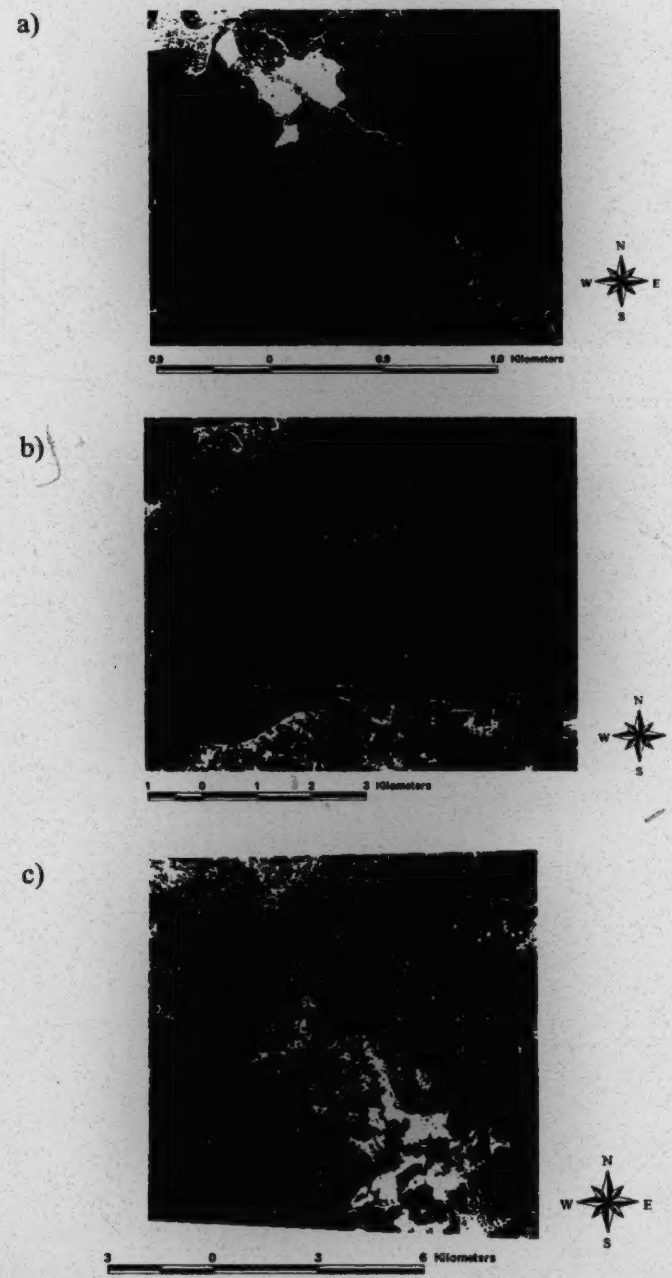
a)
N
W
E
S
0.9
0
0.9
1.8 Kilometers
b)
N
W
S
1
0
1
2
3 Kilometers
c)
N
W
E
S
3
0
3
6 Kilometers

Figure 5.2. Map of the forest structure and PAI/LAI plots in a) Chamela b) Palo Verde and c) Santa Rosa. Yellow represent the early stage, blue represents the intermediate stage and green represents the late stage.

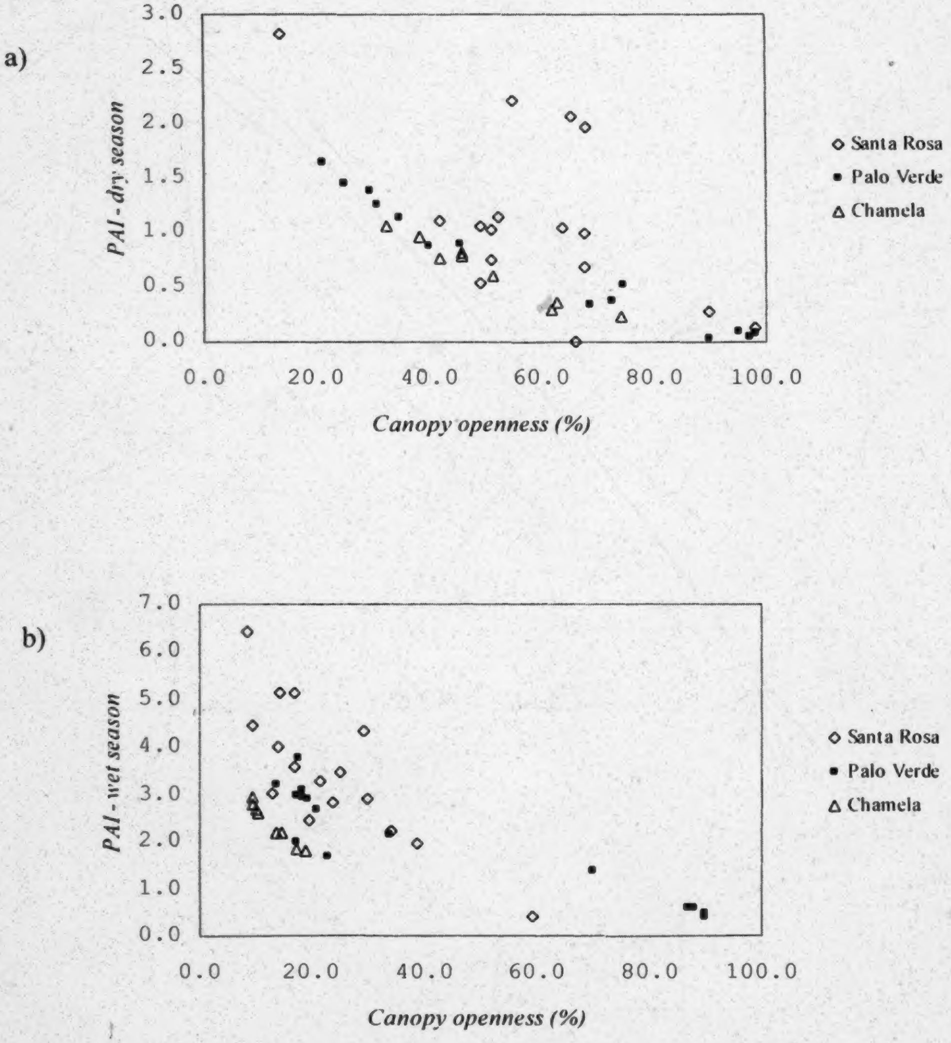

Figure 5.3 Canopy openness (%) vs. plant area index (PAI) for the dry (a) and wet (b) seasons for the three sites.

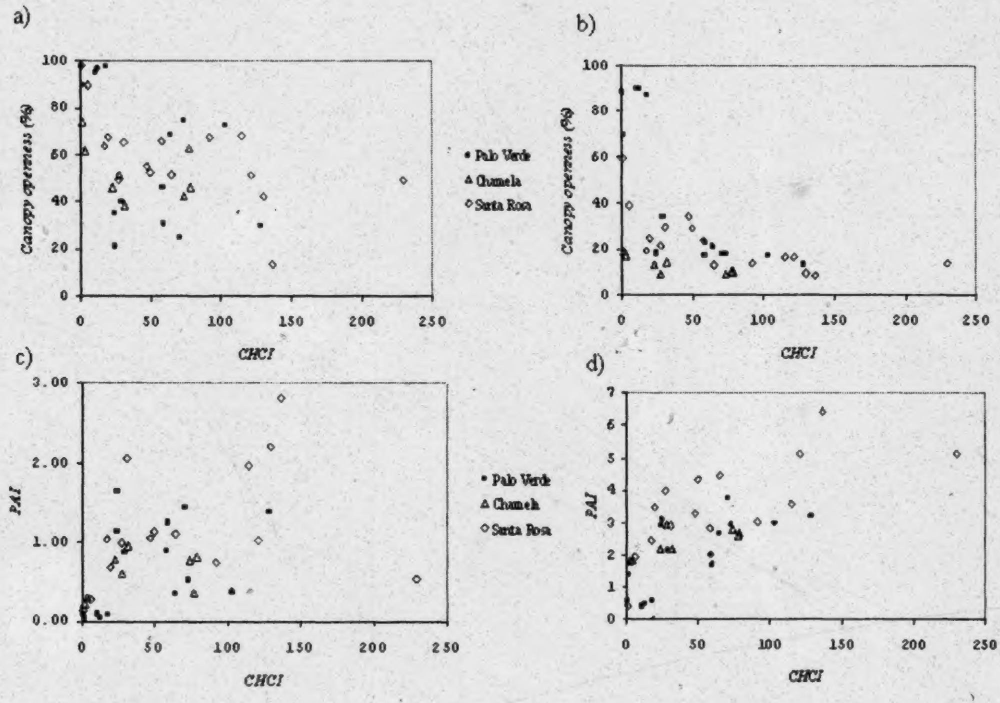

Figure 5.4 Holdridge Complexity Index (C_{HCI}) vs. PAI in the dry (a) and wet (b) seasons and vs. canopy openness (%) in the dry (c) and wet (d) seasons for the three sites.

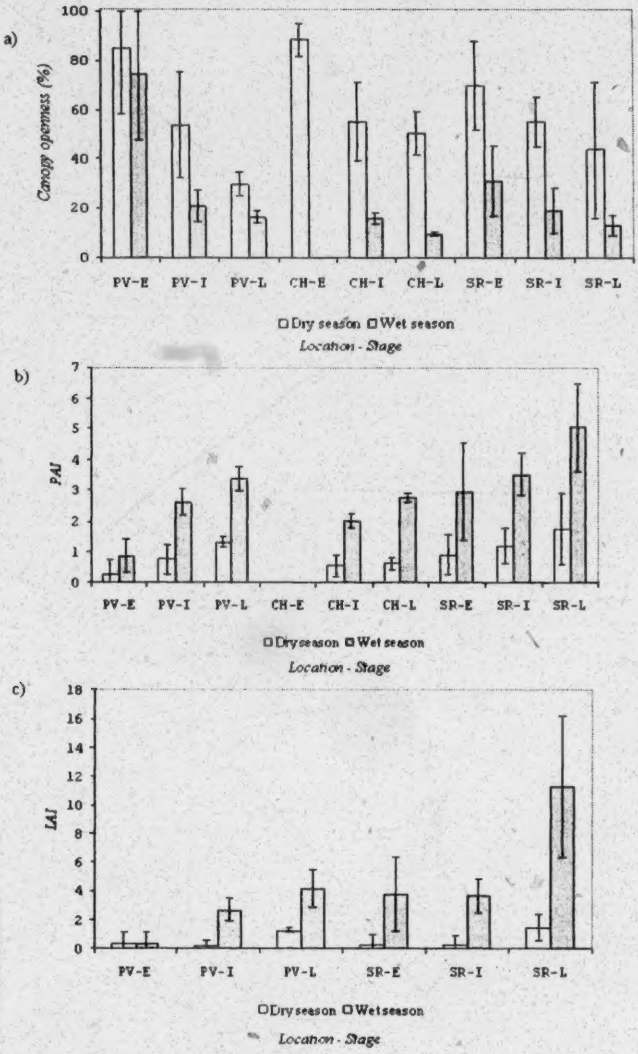

Figure 5.5. Canopy openness (%) (a), plant area index (PAI) (b) and leaf area index (LAI) (c) for the different successional stages of the three sites (Chamela – CH, Palo Verde – PV, Santa Rosa – SR). E = early stage, I = intermediate stage, L = late stage. Error bars represent one standard deviation.

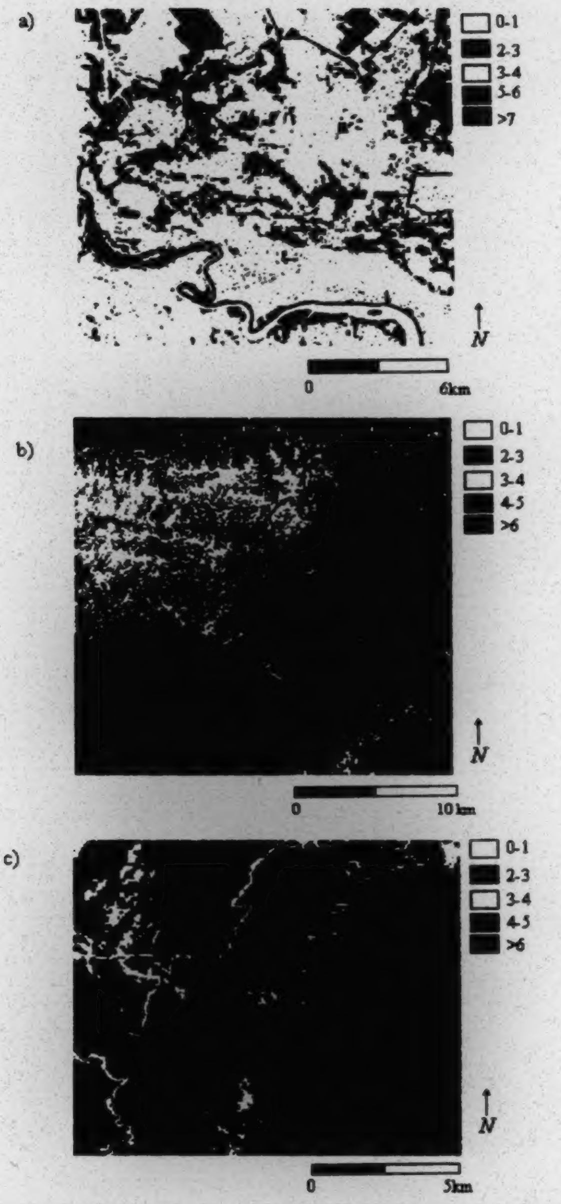
a)
0-1
2-3
3-4
5-6
>7
N
0
6km
b)
0-1
2-3
3-4
4-5
>6
N
0
10 km
c)
0-1
2-3
3-4
4-5
>6
N
0
5km

Figure 5.6. Maps of LAI (PAI for Chamela) for the three study sites created with the best fit non linear models between LAI/PAI and SVIs. a) Palo Verde, best fit SVI: MSR with a Lorentzian Cumulative Function b) Santa Rosa, best fit SVI: SAVI2 with a Lorentzian Cumulative Function c) Chamela, best fit SVI: MSR with a Lorentzian Cumulative Function.

Chapter 6: Ecological fingerprinting of ecosystem succession: estimating secondary tropical dry forest structure and diversity using imaging spectroscopy

6.1. Introduction

In the tropics, with increasing threats of forest degradation, biodiversity loss and the loss of environmental services, there has been an escalating need for in-depth studies into forest dynamics and biophysical characteristics in order to support sustainable resource development and achieve environmental protection goals (Daily et al 1997, Sanchez-Azofeifa et al. 2003, Sanchez-Azofeifa et al. 2005). Forty-seven percent of the global forest cover is in the tropics (FAO 2001) and of that, 75% is considered Dry or Moist Forest (Holdridge 1967 as cited by Murphy and Lugo 1986). However, those two ecosystems are also the most frequently disturbed (anthropogenically) and among the least protected (Mooney et al. 1995, Janzen 1986, Quesada and Stoner 2004).

Tropical forest monitoring by means of remote sensing has become both increasingly popular and feasible with the advent of satellite sensors such as Landsat 7 ETM+, ASTER, IKONOS, Quickbird, Hyperion and ALI. Monitoring efforts have generally consisted of large scale land use / land cover change (Townshend et al. 1991, Sanchez-Azofeifa et al. 2001) and the estimation of broad forest biophysical characteristics (Running et al 1986, Turner et al. 1999, Fournier et al. 2003, Thenkabail et al. 2004 among others) which are integral for understanding physiological, ecological and biogeochemical processes (Asner et al. 2002).

Forest characteristics extracted from remotely sensed data are important for global atmosphere-biosphere models (i.e. water, energy and carbon dioxide flux) (Schlerf et al. 2005), the creation of environmental policies and conservation areas (Pfaff et al. 2000, Pfaff and Sanchez-Azofeifa 2004) and secondary forest characterization (Arroyo et al. 2005). Recently, there has been considerable interest in estimating detailed forest biophysical characteristics such as leaf area index (LAI), tree height, biomass and crown diameter from remotely sensed data (Asner et al 2002, Atzberger 2004, Clark et al. 2004, Kalacska et al. 2004a, 2005b, Greenberg et al. 2005a,b, Schlerf et al. 2005, among many others). Canopy demography is then often further employed to improve harvest plans (Asner et al 2002) and assess canopy damage and recovery after selective logging (Asner et al. 2004). Nevertheless, the majority of the studies linking remote sensing and ecosystem succession in the tropics have been from the Amazon (Mausel et al. 1993, Brondozio et al. 1996, Foody et al. 1996, Steininger 1996, 2000 among others; see Castro et al. 2003 for a comprehensive review).

A second area of recent interest has been the estimation of biodiversity from remotely sensed data. In general there are two approaches: direct remote sensing of species assemblages and communities or an indirect estimation through the use of other environmental variables (Turner et al. 2003). Examples of the direct approach include species composition and land cover discrimination. The indirect approach comprises broad areas such as primary productivity, chlorophyll, climate (e.g. soil moisture, phenology) and habitat structure (e.g. topography, vertical canopy structure) (Turner et al. 2003). Some of the most important uses of the indirect approach are biomass estimation, drought prediction and mapping land cover dynamics and land cover heterogeneity (Gould 2000, Foody 2003) all of which have important impacts on biodiversity. A similar indirect measure of biodiversity is the classification (in descending order of scale) of ecoregions, ecomosaics and ecotopes (Nagendra and Gadgil 1999a). In this classification, each ecoregion has a unique community of species and environmental conditions. Ecomosaics are finer types within an ecoregion and ecotopes are characterized by an even finer spatial detail colonized by a unique species composition of a particular group such as flowering plants. At each of the levels, the classes are distinguishable by remote sensing and are significantly different from each other in composition with respect to the different entities at the next lower level (Nagendra and Gadgil 1999a,b). Measures of vegetation biodiversity (i.e. indices of species richness and evenness) have been linked to remotely sensed data most often through the classification of the forest based on the similarity of tree species or similarity in landscape elements (Menon and Bawa 1997, Nagendra and Gadgil 1999a,b, Nagendra 2001, Foody and Cutler 2003). At the landscape scale the results are employed for conservation science and management decisions (Arroyo-Mora and Chazdon 2005). However, in many studies, the remotely sensed data has been underutilized by the calculation of vegetation indices and the use of surrogates (i.e. biomass, land cover type and heterogeneity) for species richness estimations (Foody and Cutler 2003). An important drawback to such studies is the non-transferability of results from one area to another, even within ecosystem types (Foody et al. 2003). Another important consideration is the overuse of remotely sensed data or the acceptance of relatively weak correlations between biophysical characteristics or floristic diversity and spectral reflectance data (Tuomisto et al. 2003).

In this study we use the concept of an "ecological fingerprint" as a "*comprehensive spatial description of forest structure and floristic diversity*". Secondary forests are becoming more prominent in the landscape in most Neotropical countries, and therefore, are the future of forest management and monitoring. We incorporate their inherent heterogeneity into the ecological fingerprint and develop models that can monitor the dynamics of their changes over time. Until the acceptance that secondary forests could act as positive carbon sinks (Brown and Lugo 1990), they were generally regarded as inferior to old-growth. Furthermore, the characterization of these forests has generally been through "age since abandonment" chronosequences (Lucas et al. 2000). However, as Arroyo-Mora et al. (2005) have shown, successional stages quantified by forest structure, are a more accurate categorization especially for the tropical dry forest and especially for studies incorporating remotely sensed data. Hence the creation of models to examine individual structural and diversity elements (e.g. canopy height, basal area, etc. that quantify successional stage) will produce "snapshots" of their regeneration state and a method for monitoring over time.

Here, we examine direct forest structure and biodiversity (through the Shannon diversity index) estimation from satellite imagery. We address the inference and mapping of tropical dry forest biophysical characteristics (i.e. structure), biomass and species richness directly from hyperspectral remote sensing imagery acquired over three seasons: wet, transition and dry. We explore common techniques such as spectral vegetation indices and principal component analysis and the application of wavelet transforms, a common practice in the signal processing community, with various types regression models and neural networks for inference. Through these methods the potential for monitoring changes in forest structure and diversity through time is shown; applications for which range from testing theoretical regeneration hypotheses to assessing habitat quality for fauna or flora.

6-2. Methods

6-2.1 Study area

The study site is located in the Santa Rosa National Park (Guanacaste Province), a World Heritage Site, in northwestern Costa Rica (10 ° 48' 53"N, 85° 36' 5"4W). Over time, the national park has come to be known as the Santa Rosa sector of a larger conservation area called the Área de Conservación Guanacaste (ACG). This area receives an average of 1,500mm of precipitation per year with a 6 month dry season (December to May) where the majority of the vegetation is deciduous. We refer to this area as a seasonally dry neotropical forest based on the definition from Sanchez-Azofeifa et al. 2005: an *area with a vegetation type dominated by deciduous trees located in an area with a mean temperature >25°C, a total annual precipitation range of 700-2000mm and three or more dry months (precipitation <100mm).* The vegetation in Santa Rosa is a mosaic of secondary forest in various successional stages with interspersed pastures (Janzen 1988a,b, 2000, Kalacska et al. 2004b). The land use history, intensity of past uses and discrete anthropogenic fire history of Santa Rosa is highly varied. Some of the more common past land uses for this area were pasture, dryland rice, timber extraction, agriculture and banana plantation (Kalacska et al. 2004b). Therefore, the structure of the regenerating vegetation has been greatly affected by the various land use histories of the area. Taking this into account we categorize the forest by its horizontal and vertical structures when sampling the vegetation and describing the successional stages. We refer to three successional stages for the vegetation: early, intermediate and late as described by Kalacska et al. (2004b), Arroyo-Mora et al. (2005) and Kalacska et al. (2005a,b). The early stage is composed of many small trees, shrubs and open areas (heterogeneous canopy), the intermediate stage is composed generally of deciduous trees with lianas forming a substantial component of the canopy and the late stage is composed of two canopy strata including dominant canopy trees, shade tolerant species and overlapping crowns. Structure and floristic composition was measured in twenty-six 20 x 50m (0.1ha) plots (10 early, 10 intermediate, 6 late) for woody stems with a diameter-at-breast-height (DBH) ≥5cm (Kalacska et al. 2004b). Total above ground live biomass was calculated from the following allometric equation from Brown (1997):

$$\mathrm{ATB} = \exp\{-1.996+2.32(\ln D)\} \qquad (1)$$

where biomass is expressed in kilograms of dry mass and D is DBH in centimeters. From the structural variables we calculated the Holdridge Complexity Index (HCI) from Holdridge (1967):

$$HCI = \frac{HGDS}{1000} \qquad (2)$$

where H is canopy height (m), G is basal area (m^2/ha), D is stem density (No./0.1ha) and S is species density (No./0.1ha). Being a quantitative index, HCI provides a more objective measure of overall forest physiognomy than verbal descriptions or single structural variables. To estimate floristic diversity we us the Shannon diversity index (H') (Magurran 2004). The structural and floristic measures are summarized in Table 6.1.

6-2.2 Image processing

The satellite images used in this study were three atmospherically corrected Hyperion scenes (220 bands, 30m spatial resolution) acquired March 2002, December 2002 and January 2003 as shown in Fig. 1 with the leaf phenological cycle. The pixel values for each of the twenty-six sites were extracted from each image in a 3x3 pixel window around the centre of each plot. Initial pre-processing consisted of the removal of the bands with a low signal-to-noise ratio (<430nm and >2400nm) and the areas of water absorption (centered around 1400nm and 1900nm) resulting in a total of 153 bands for the analysis.

Subsequently we followed four different data reduction approaches: calculation of narrow band spectral vegetation indices (SVIs), principal component analysis (PCA), discrete wavelet transform (WT) and calculation of energy features from the discrete wavelet transform (WT_{EF}). The six SVIs we examined are the Normalized Difference Vegetation Index (NDVI) (Sims and Gamon 2002), Canopy Normalized Difference Vegetation Index (Sims and

Gamon 2003), Single Ratio (Sims and Gamon 2002), Canopy Single Ratio (Sims and Gamon 2002), Modified Single Ratio (Chen 1996), and Canopy Structure Index (Sims and Gamon 2003) (Table 6.2).

Principal component analysis (PCA) is a common linear technique for reducing the dimensions of data (i.e. simplifying) and highlighting the inherent variation (Schowengerdt 1996). However, it has been shown that for certain data distributions where within-class variance dominates between-class variance, PCA is not an optimal feature extraction method for target detection applications (Cheriyadat and Bruce 2003) and is sensitive to noise (Schowengerdt 1996).

Wavelet transform is a time-scale signal analysis technique that may reveal features of a signal (e.g. reflectance spectrum) such as trends or discontinuities that other techniques may miss (Misiti et al. 1996). The wavelet transform process breaks up a signal into shifted and scaled versions of the original waveform being used (i.e. mother wavelet). The majority of these waveforms tend to be irregular and asymmetric. With discrete wavelet transforms, signals are analyzed over a set of discrete scales (i.e. 2^j, j=1,2,3….n). Wavelet basis functions are calculated for spectral data by shifting and scaling the mother wavelet (basis function) across the data. The result is a set approximation (cA_j) (low pass filter) and detail (cD_j) (high pass filter) coefficients (Mallat 1989, Misiti et al. 1996, Li et al. 2001). We conducted a discrete wavelet transform of the Hyperion spectra using a mother wavelet from the Daubechies family (db3). This multilevel decomposition (7 levels) was implemented in Matlab v.6.5 resulting in 7 detail coefficients (cD_{1-7}) and the largest approximation coefficient

(cA_7) with a combined length of 182 elements.

Our final reduction approach consisted of calculating the scalar energy feature vector of the detail and approximation coefficients from the wavelet decomposition described above using the following formula (Bruce et al. 1999, Li et al. 2001, Pu and Gong 2004):

$$F_j = \sqrt{\frac{1}{K}\sum_{K=1}^{K} W_{jk}^2} \qquad (3)$$

where K is the number of coefficients at level j, W_{jk} is the kth coefficient at level j. The length of the vector is (j+1) (i.e. the detail coefficients and the approximation coefficient) where j is the maximum number of decomposition levels. With this method, the original 153 dimensions of the data have been reduced to 8.

Following data reduction various regression techniques (linear, non-linear, stepwise and generalized neural network) were employed with the reduced data to infer the forest characteristics from the images. To test the effectiveness of the various models we used a cross validation method (Isaaks and Srivastava 1989) to assess the validity of the models. This "leave-one-out" validation technique was used due to the limited number of data points (sites). The withheld data points were sequentially estimated by the models (best fit models reduction – inference combination from best overall models) to produce an overall estimation of the fit. Twenty-six separate models were created for each variable, each with twenty-five data points. These models were then used to estimate the value of the data point that was left out. The model (i.e. data reduction technique with regression model) with the best fit (from the validation) was then run on a pixel by pixel basis over the image (using Matlab v.6.5) to create maps of the biophysical characteristics and floristic diversity.

6-3. Results

For most of the 26 sites, the most distinct reflectance spectrum is the one from March (dry season). For nearly all early stage sites a higher reflectance in the near infrared is observed in comparison to the other two time periods (December and January). For the intermediate and late stages, the most distinct difference is the lack of the green peak and red absorption valley (also seen in the early stage).

None of the vegetation indices had a strong relationship with any of the biophysical variables for any of the images (March, December and January). The values for the coefficient of determination were between 0.27 and 0.56 for the SVIs with each image. The only exception was canopy height which had relationships with an R^2 consistently between 0.62 and 0.66 for all images with all SVIs except CSI (which had R^2 between 0.48 and 0.56 for the three images). For the PCA reduction technique, the relationships following regression were very similar to what was found with the SVIs. For example for the January image, the best model was with canopy height (R^2=0.50). And for March and December the best models were with HCI (R^2=0.65) and canopy height (R^2=0.56) respectively. The results from the regression models with the wavelet energy feature vectors were also similar to the SVIs and PCA. The models from all of the biophysical characteristics for December and January ranged from $R^2=0.20$ for species density (January) to $R^2 = 0.68$ for canopy height (January). For the March image the models were weaker with a range of $R^2 = 0.05$ (stem density, species density, Shannon diversity, HCI) to $R^2=0.45$ for biomass.

When specific elements from the approximation and detail coefficients were selected from the wavelet decomposition using stepwise regression the models for all variables improved for each image with both a final multiple regression or generalized neural network regression (i.e.$R^2>0.8$). Consequently, we performed the cross-validation to compare the multiple regression versus the generalized neural network regression. The final overall best model for biomass, Shannon diversity, canopy height, Holdridge Complexity Index and basal area was the multiple regression using the elements from the wavelet decomposition approximation and detail coefficients selected by the stepwise procedure from the March image (Table 6.3, Figure 2). There was no suitable model following validation for stem or species densities.

For the sites that were close to the mean value of the biophysical characteristics, the neural network regression had the lowest error in the cross-validation. However, for the sites that were outliers from the mean the error from the cross-validation on the neural network regression was very large. For the multiple regression the error from the cross-validation remained fairly constant for all sites regardless of whether they were close to the mean, thus less sensitive to outliers This is an important consideration because as can be seen in Table 6.1, there is a wide range with several outliers for all biophysical characteristics. In summary, the most robust model for estimating the biophysical characteristics and diversity was wavelet transform decomposition, followed by a stepwise regression from the March (dry season) image. Figure 3 illustrates the features that were chosen for biomass. The majority of the features were from cD1 with two features chosen from cD4. Similar features were also chosen for HCI, canopy height, basal area and Shannon diversity. However, at present we cannot directly tie the features chosen from the wavelet decomposition to specific wavelengths of the spectra to fully understand physical meaning of the chosen features. Subsequently as illustrated in Figure 2, we mapped canopy height, biomass, basal area, Shannon diversity and HCI (Figure 4).

6-4. Discussion

Our results highlight the importance of considering the spectro-temporal domain – season of image acquisition when mapping variables that define ecological succession for the tropical dry forest. Utilizing the methodology presented here, the *dynamics* – the changes over time (e.g. 5 year change) of the structure and composition of the forest can be monitored from snapshots of variables that comprise the forest's "fingerprint" such as yearly changes in basal area. While this methodology only provides an index of species diversity and does not identify individual species given the course spatial resolution of our data, results from Clark et al. (2005), Castro and Sanchez-Azofeifa (2005), Castro et al. (in press) and Zhang et al. (subm) show that individual species from the tropics can be identified spectrally using much finer spatial resolution imagery. Including such identifications (by means of finer spatial resolution data) and monitoring species turnover through time would add another dimension to the concept of the ecological fingerprint. The importance of the spectro-temporal domain (i.e. season) is also emphasized by Castro et al. (in press) who illustrate the changes to the spectral reflectance of individual tropical species over time. Similarly, for a temperate forest located in the Pacific Northwest of the United States, Roberts et al. (2004) show a trend between stand attributes (such as age, composition and structure) and hyperspectral canopy reflectance along with the changes through forest succession. Roberts et al. (2004) also reaffirm the utility of remote sensing to illustrate the spatial patterns of stands in various stages of succession.

The relationships between the structure. diversity and the imagery were the most robust when the spectra were decomposed by means of a wavelet analysis to highlight subtle spectral features. It is also clear from the results that there is much redundant information in the spectra. The use of select components of the wavelet decomposition chosen by means of a stepwise regression filtered the spectra in order to use only the most significant features. This type of "feature selection" on the product of the wavelet decomposition allowed access to the most meaningful features of the reflectance spectra. Feature selection has been an important aspect in the analysis of hyperspectral data (Castro-Esau et al. 2004, Clark et al. 2005,De Backer et al. 2005, Huang and He 2005); here we emphasize its combination with wavelet analysis to extract subtle spectral features (Mallat 1989, Misiti et al. 1996, Bruce et al 1999, Li et al. 2001, Bruce et al. 2002). These findings tend to agree with others such as Lee et al. (2004) and Thenkabail et al. (2004) that the large number of narrow bands of hyperspectral data is an advantage for the estimation of canopy characteristics.

The results from the vegetation indices and the principal component analysis are consistent with what was found by Schlerf et al. (2005) using both broadband and narrow band SVIs to estimate stem biomass, volume and LAI in a temperate environment. The strength of the relationships are also similar to the strength of the best correlations reported by Tuomisto et al. (2003) who linked understory floristic patterns to Landsat imagery from the Ecuadorian Amazon. Our lack of an adequate model for estimating stem density is contrary to Ingram et al. (2005) who found a strong inverse relationship between NDVI and stem density in a tropical secondary forest in Madagascar. In the aforementioned analysis a subset of extreme pixel values was used. Because of the inherent heterogeneity within each successional stage and the landscape as a whole for each structure and diversity characteristic it is important to use an inference technique that is not overly influenced by outliers.

The early stage, which is highly variable in its canopy structure, has a dynamic understory through the seasons. In the wet season the small (DBH<5cm) treelets, shrubs and herbs along with grass (as in pastures) form a thick understory confounding the spectral signature in the open areas and filling the canopy gaps of the early and intermediate stages which begins to resemble that of a mature forest canopy (Kalacska et al. *subm*). In the dry season however, the stages of forest development are readily separable. Kalacska et al. (2004b) found that the majority of the structural variables are distinct for the successional stages in the study area.

And thus the reason for the strongest relationships with spectra from the March image is that as a dry season image the various stages of forest regeneration are clearly highlighted in the spectral response (Arroyo-Mora et al. 2005) and the confusion from green herbaceous understory vegetation is minimized. As illustrated in Figure 1, the timing of this image corresponds to minimal LAI. It also corresponds to the point in the leaf phenological cycle where the woody component of the canopy has the greatest contribution to reflectance. For the tropical dry forest in Santa Rosa N.P. Kalacska et al. (2005a) show that because of the nature of the canopy and the increased number of lianas in the intermediate successional stage has a woody-area-index more than double that of the early and late stages. Arroyo-Mora et al. (2005) indicate for the same study area in the dry season the numerous canopy gaps in the early stage (lowest wood-area index) allow for a greater contribution of the dry grass and soil. It is intuitive that in the wet season the reflectance spectra for all stages are dominated by leaves. In the dry season however, the quantitative contribution of each element seen by the sensor (e.g. exposed soil, dry leaf litter, various types of bark, retained leaves, etc.) to the reflectance spectra is unknown. We can only provide anecdotal evidence based on field observations. In the early stage with several large canopy gaps, there is an increased amount of dry grass, leaf litter and soil exposed along with bark from leafless trees. In the intermediate stage the increased amount of woody biomass from lianas covering the canopy limits ground exposure and it is likely that various types of bark are the major constituents of the spectra. In the late stage leaves are retained by some trees and then reflectance spectra would tend to be a mixture (most likely nonlinear) of leaves, exposed bark and limited exposed soil and leaf litter.

We stress that forest structure and diversity analyses with remotely sensed data must focus on the canopy (i.e. the surface that is reflecting the radiation measured by the sensors) which in the dry season may be a complex mixture of various targets. It is inappropriate to assume however, that by using canopy reflectance reliable relationships can be established directly with subcanopy elements such as understory species richness or structures that are covered by a mature homogeneous canopy.

Maps such as the ones in Figure 4 are a valuable resource for the management and conservation of this ecosystem, especially when considered in the context of being a comprehensive spatial snapshot of the forest structure and diversity. Simple forest/non forest maps do not offer the detail necessary to assess forest degradation (Ingram et al. 2005) or recuperation. Therefore, on a regional scale, by illustrating the characteristics of the forest, areas can be more precisely assessed and prioritized for conservation than from only LAI or forest/non-forest maps. The changes in the characteristics of the forest (i.e. HCI, basal area, Shannon diversity, etc) are the details needed to properly assess the condition of the forest within a specific area.

The analysis of interpretation of remotely sensed data as presented here in the form of structure and diversity components provide the opportunity to explore one of the most prevalent questions in forest regeneration: scale. As discussed by Webb et al. (1972), scale and thus the appearance of specific patterns or distributions in the landscape are a matter of perception driven by scale. The rapid analysis on a large scale of numerous structure and diversity variables could lead to the discovery of the spatial dynamics of the neotropical dry forest at numerous scales from the microscale plot level to an entire region. Furthermore expanding these analyses to include high spatial resolution airborne imagery (e.g. HyMap) could potentially improve the models. HyMap (Cocks et al. 1998) collects hyperspectral images with 128 bands from 400-2500nm with a spectral bandwidth of 15-20nm.

Models incorporating high resolution hyperspectral data such as Hymap may further improve our understanding of the dynamics of secondary tropical dry forest regeneration. Analyzing changes in the structural and diversity components the distribution of individual species may be monitored to expand on observations such as the role of past anthropogenic disturbance along with random thinning, dispersal modes and colonization rates on the clumped distribution of tropical dry forest trees (Hubbell 1979). Kalacska et al. (2004b) found that the pattern of species richness through the stages in Santa Rosa N.P. were partly consistent with Connell's (1978) ecological succession hypothesis. With the structure and diversity models constructed, long term remotely sensed monitoring the area may reveal whether that pattern is consistent or whether the area follows a different trend over time. Stern et al. (2002) found that economically valuable species did not regenerate in disturbed areas of another tropical dry forest in Costa Rica (Palo Verde) whereas Kennard (2002) and Gould et al. (2002) reported the contrary. By including high spatial resolution hyperspectral imagery it would allow for expanding the scale of the studies by Castro et al. (in press), Clark et al. (2005) and Zhang et al. (subm) to map common (e.g. *Rehdera trinervis, Guazuma ulmifolia, Semialarium mexicanum*) and/or endangered and valuable (e.g. *Guaiacum sanctum, Swietenia macrophylla, Platymiscium pleiostachyum*) tree species from the tropical dry forest on a regional level and follow their patterns of regeneration (or lack thereof).

6-5. Conclusions

In this study we explored the use of Hyperion hyperspectral imagery from three seasons to estimate canopy biophysical parameters and floristic diversity. Data reduction and inference techniques were compared over the dry, wet and transition seasons and consequently we conclude the following:

- The dry season image produced the optimal results for modeling
- A wavelet decomposition followed by stepwise regression to construct a model with only the most significant elements produced the best overall model following validation
- The subtle spectral features detected by the wavelet decomposition are required for estimating dry forest biophysical characteristics

For future studies it is also important to investigate the various contributors to the reflectance spectra in the dry season in this ecosystem to understand their respective importance in the various stages. In addition, the examination of this model in other dry and wet forest ecosystems would be important in order to investigate how the models change based on forest type (e.g.

would neural networks produce better results in more homogeneous ecosystems?). In drier ecosystems such as Chamela in Mexico, the forest structure poses different challenges in comparison to Santa Rosa (i.e. the structural variables do not follow the same trends for the successional stages) (Kalacska et al. 2005b). Wet forest ecosystems with denser canopies and less dramatic changes in leaf phenology; thus possibly more subtle changes in the canopy spectra, would also pose various challenges. Therefore, the testing of this model in various ecosystems is necessary to understand the limits of its utility and the transferability of the spectro-temporal domain concept from one ecosystem to another.

6-6. References

Arroyo-Mora J.P., Chazdon R. 2005. Natural forest management plans in Costa Rica: a potential framework for assessing tree biodiversity. Frontiers in tropical biology and conservation, Association for tropical biology and conservation annual meeting. Ublerlândia -MG, Brazil. pp. 53.

Arroyo-Mora J.P., Sanchez-Azofeifa G.A., Kalacska M., Rivard B., Calvo-Alvarado J.C., Janzen D., 2005. Secondary forest detection in a Neotropical dry forest using Landsat 7 ETM+ and IKONOS imagery. Biotropica Accepted.

Asner G.P. Keller M., Pereira R., Zweede J.C., Silva J.N.M. 2004. Canopy damage and recovery after selective logging in Amazonia: Field and satellite studies. Ecological Applications 14(4): S280-S298 Suppl. S.

Asner G.P., Keller M., Pereira R., Zweede J.C., 2002. Remote sensing of selective logging in Amazonia - Assessing limitations based on detailed field observations, Landsat ETM+, and textural analysis. Remote sensing of environment 80, 483-496.

Atzberger C., 2004. Object-based retrieval of biophysical canopy variables using artificial neural nets and radiative transfer models. Remote sensing of environment 93, 53-67.

Brondizio E., Moran E., Mausel P., Wu Y. 1996. Land cover in the Amazon Estuary: linking of the Thematic Mapper with botanical and historical data. Photogrammetric Engineering and Remote Sensing, 62:921-929.

Brown S., Lugo A.E. 1990. Tropical secondary forests. Journal of tropical ecology 6:1-32.

Brown S., 1997. Estimating biomass and biomass change of tropical forests: a primer. Rome, FAO Forestry Paper no. 143.

Bruce L.M, Morgan C., Larsen S., 1999. Automated detection of subpixel hyperspectral targets with continuous and discrete wavelets. IEEE Transactions on Geoscience and Remote Sensing 37, 2217-2226.

Bruce L.M., Koger C.H., Jiang L..2002. Dimensionality reduction of hyperspectral data using discrete wavelet transform feature extraction *IEEE Transactions on Geoscience and Remote Sensing* vol. 40 pp. 2331-2338.

Castro K.L., Sanchez-Azofeifa G.A., Rivard B. 2003. Monitoring secondary tropical forests using space-borne data: implications for Central America. *International Journal of Remote Sensing* 24:1853-1894.

Castro-Esau K., Sanchez-Azofeifa G.A., Caelli T. 2004. Discrimination of lianas and trees with leaf-level hyperspectral data *Remote Sensing of Environment* vol. 90 pp. 353-372. 2004.

Castro-Esau K., Sanchez-Azofeifa G.A. 2005. Inter and intra-specific variability in leaf optical properties of Mesoamerican trees. Frontiers in tropical biology and conservation, Association for tropical biology and conservation annual meeting. Ublerlândia -MG, Brazil. pp. 24.

Castro-Esau K., Sanchez-Azofeifa G.A., Rivard B., Wright S.J., Quesada M. Variability in leaf optical properties of Mesoamerican trees and the potential for species classification. *American Journal of Botany*. Submitted 2005.

Chen J.M. 1996. Evaluation of vegetation indices and a modified simple ratio for Boreal applications. Canadian Journal of Remote Sensing 22:229-241.

Cheriyadat A., Cruce L.M., Why principal component analysis is not an appropriate feature extraction method for hyperspectral data. Geoscience and remote sensing symposium IGARSS '03. 2003. IEEE International .

Clark D.B., Read J.M., Clark M.L., Cruz A.M., Dotti M.F., Clark D.A., 2004. Application of 1-M and 4-M resolution satellite data to ecological studies of tropical rain forests. Ecological Applications 14, 61-74.

Clark ML, Roberts DA, Clark DB. 2005. Hyperspectral discrimination of tropical rain forest tree species at leaf to crown scales. *Remote Sensing of Environment*

96 375-398.

Cocks T., Jenssen R., Stewart A., Wilson I., and Shields T. 1998. The HyMap airborne hyperspectral sensor: the system, calibration and performance. First EARSeL Workshop on Imaging Spectroscopy. Paris, EARSeL.

Connell J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.

Daily G.C., Alexander S., Erlich P.R., Goulder L., Lubchenko J., Matson P.A., Mooney H.A., Postel S., Schneider S.H., Tilman D., Woodwell G.M., 1997. Ecosystem services: benefits supplied to human societies by natural ecosytems. In:Issues in Ecology, number 2. Ecological Society of America, Washington, DC, pp. 1-16.

De Backer S., Kempeneers P., Debruyn W., Scheunders P. A band selection technique for spectral classification. 2005 *IEEE Geoscience and Remote Sensing Letters* vol 2(3) pp. 319-323.

FAO, 2001. COFO-2000/INFS-Global forest resources assessment 2000. FAO of the United Nations, Rome.

Foody D.M., Boyd D.S., Cutler M.E.J., 2003. Predictive relations of tropical forest biomass from Landat TM data and their transferability between regions. Remote sensing of environment 85, 463-474.

Foody G.M., 2003. Remote sensing of tropical forest environments: towards the monitoring of environmental resources for sustainable development. International journal of remote sensing 24, 4035-4046.

Foody G.M, Cutler M.E.J., 2003. Tree biodiversity in protected and logged Bornean tropical rainforests and its measurement with satellite remote sensing. Journal of Biogeography 10, 1053-1066.

Foody G.M. Palubinskas G., Lucas R.M., Curran P.J. Honzak M., Amaral I.D. 1996. Identifying terrestrial carbon sinks: classification of successional stages in regenerating tropical forest from Landsat TM data. Remote sensing of environment 55:205-216.

Fournier R.A., Mailly D., Walter J.-M., Soudani K., 2003. Measurement of forest structure. In: Wulder M., Franklin S. (Eds.), Methods for remote sensing of forests: Concepts and case studies. Kluwer, New York.

Gould W., 2000. Remote sensign of vegetation, plant species richness and regional biodiversity hotspots. Ecological applications 10, 1861-1870.

Gould K.A., Fredricksen T.S., Morales F., Kennard D., Putz F.E. Mostacedo B., Toledo M. 2002. Post-fire tree regeneration in lowland Bolivia: implications for fire management. Forest Ecology and Management. 165:225-245.

Greenberg J.A., Dobrowski S.Z., Ustin S.L., 2005. Shadow allometry: Estimating tree structural parameters using hyperspatial image analysis. Remote sensing of environment 97, 15-25.

Greenberg J.A., Kefauver S.C., Stimson H.C., Yeaton C.J., Ustin S.L., 2005. Survival analysis of a neotropical rainforest using multitemporal satellite imagery. Remote sensing of environment 96, 202-211.

Holdridge L.R., 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica.

Huang R., He M. Band selection based on feature weighting for classification of hyperspectral data. 2005 *IEEE Geoscience and Remote Sensing Letters*. vol. 2(2) pp.156-159.

Hubbell S.P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203: 1299-1309.

Ingram J.C., Dawson T.P., Whittaker R.J. Mapping tropical forest structure in Southeastern Madagascar using remote sensing and artificial neural networks. 2005. *Remote Sensing of Environment* vol.94 pp. 491-507.

Isaaks EH, Srivastava RM. 1989. *Applied Geostatistics*. Oxford University Press, Oxford

Janzen D.H., 2000. Costa Rica's Area de Conservacion Guanacaste: a long march to survival through non-damaging biodevelopment. *Biodiversity* 1, 7-20.

Janzen D.H., 1988a. Guanacaste National Park: Tropical ecological and biocultural restoration. In: Cairns J.J. (Ed.)., Rehabilitating damaged ecosystems, Vol II. CRC Press, Boca Raton, Florida, pp. 143-192.

Janzen D.H., 1988b. Management of habit fragments in a tropical dry forest: Growth. *Annals of the Missouri Botanical Garden* 75, 105-116.

Janzen D.H., Washington DC. 1986. Tropical dry forests: the most endangered major tropical ecosystem. In: Wilson E.O. (Ed.)., Biodiversity . National Academy Press, pp. 130-137.

Kalacska M., Calvo-Alvarado J.C., Sanchez-Azofeifa G.A., 2005a. Calibration and assessment of seasonal changes in leaf area index of a tropical dry forest in different stages of succession. *Tree Physiology* 25, 733-744.

Kalacska M., Sanchez-Azofeifa G.A., Calvo-Alvarado J.C., Rivard B., Quesada M., 2005b. Effects of season and successional stage on leaf area index and spectral vegetation indices in three Mesoamerican tropical dry forests. *Biotropica*

In press.

Kalacska M., Sanchez-Azofeifa G.A., Rivard B., Calvo-Alvarado J.C., Journet A.R.P., Arroyo-Mora J.P., Ortiz-Ortiz D. 2004a. Leaf area index measurements in a tropical moist forest: A case study from Costa Rica. *Remote Sensing of Environment* 91:134-152.

Kalacska M., Sanchez-Azofeifa G.A., Calvo-Alvarado J.C., Rivard B., Quesada M., Janzen D.H., 2004b. Species composition, similarity and diversity in three successional stages of tropical dry forest. *Forest Ecology and Management* 200, 227-247.

Kalacska M., Sanchez-Azofeifa G.A., Rivard B., Calvo-Alvarado J.C., Quesada M. Quantification of tropical forest extent and payments for environmental services from satellite imagery. *Global Change Biology*. Submitted 2005.

Kennard D.K. 2002. Secondary forest succession in a tropical dry forest: patterns of development across a 50-year chronosequence in lowland Bolivia. Journal of Tropical Ecology. 18:53-66.

Lee K.S., Cohen W.B., Kennedy R.E., Maiersperger T.K., Gower S.T. Hyperspectral versus multispectral data for estimating leaf area index in four different biomes. Remote Sensing of Environment 91:508-520.

Li J., Bruce L.M., Byrd J., Barnett J.2001. Automated detection of pueraria Montanta (Kudzu) through Haar analysis of hyperspectral reflectance data. *IEEE International Geosciences and Remote Sensing Symposium, Sydney Australia July 9 – 13.*

Lucas R.M., Honzak M., Curran P.J., Foody G.M., Milne R., Brown T., Amaral S. 2000. Mapping the regional extent of tropical forest regeneration stages in the Brazilian Legal Amazon using NOAA AVHRR data. *International Journal of Remote Sensing, 21*, 2855-2881.

Magurran A.E., 2004. Measuring biological diversity. Blackwell Science, Malden MA.

Mallat S.G. 1989. A theory for multiresolution signal decomposition: the wavelet representation. *IEEE Transactions on Pattern Analysis and Machine Intelligence* vol. 11 pp. 647-693.

Mausel P., Wu Y., Li Y., Moran E.F., Brondizio E.S. 1993. Spectral identification of successional stages following deforestation in the Amazon. Geocarto International 4:61-71.

Menon W., Bawa K.S. 1997. Applications of geographic information systems, remote-sensing, and a landscape ecology approach to biodiversity conservation in the Western Ghats. Current Science 73(2): 134-145.

Misiti M., Misiti Y. Oppenheim G., Poggi J.M. 1996. *Wavelet Toolbox User's Guide* Natick MA. The Mathworks Inc.

Mooney H.A., Bullock S.H., Medina E., 1995. Introduction. In: Bullock S.H., Mooney H.A., Medina E. (Eds.), Seasonally dry tropical forests. Cambridge University Press, pp. 1-8.

Murphy P.G., Lugo A.E., 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. Biotropica 18, 89-96.

Nagendra H., 2001. Using remote sensing to assess biodiveristy. International journal of remote sensing 22, 377-400.

Nagendra H., Gadgil M., 1999a. Biodiversity assessment at multiple scales: linking remotely sensed data with field information. Proceedings of the national academy of science 96, 9154-9158.

Nagendra H, Gadgil M., 1999b. Satellite imagery as a tool for monitoring species diversity: an assessment. Journal of applied ecology 36, 388-397.

Pfaff A.S.P., Kerr S., Hughes R.F., Liu S., Sanchez-Azofeifa G.A., Schimel D., Tosi J., Watson V., 2000. The Kyoto protocol and payments for tropical forests: An interdisciplinary method for estimating carbon-offset supply and increasing the feasibility of a carbon market under the CDM. Ecological Economics 35, 203-221.

Pfaff A.S.P., Sanchez-Azofeifa G.A., 2004. Deforestation pressure and biological reserve planning: a conceptual approach and an illustrative application for Costa Rica. Resource and Energy Economics 26, 237-254.

Pu R., Gong P., 2004. Wavelet transform applied to EO-1 hyperspectral data for forest LAI and crown closure mapping. Remote sensing of environment 91, 212-224.

Quesada M., Stoner K.E., 2004. Threats to the conservation of the tropical dry forest in Costa Rica. In: Frankie G.W., Mata A., Vinson S.B. (Eds.), Biodiversity conservation in Costa Rica: Learning the lessons in a seasonally dry forest. University of California Press, Berkely, CA, pp. 266-280.

Richter R., Muller A., Heiden U. 2002. Aspects of operational atmospheric correction of hyperspectral imagery. International Journal of Remote Sensing. 23:145-157.

Roberts D., Ustin S.L., Ogunjemiyo S., Greenberg J., Dobrowski S.Z., Chen J., Hinckley T.M. 2004. Spectral and structural measures of Northwest forest vegetation and leaf and landscape scales. Ecosystems 7:545-562.

Running S.W., Peterson D.L., Spanner M.A., Teuber K.B., 1986. Remote sensing of coniferous forest leaf area. Ecology 67, 273-276.

Sanchez-Azofeifa G.A., Daily G.C., Pfaff A.S.P., Busch C., 2003. Integrity and isolation of Costa Rica's national parks and biological reserves: examining the dynamics of land-cover change. Biological Conservation 109, 123-135.

Sanchez-Azofeifa G.A., Harriss R.C., Skole D.L., 2001. Deforestation in Costa Rica: A quantitative analysis using remote sensing imagery. Biotropica 33, 378-384.

Sánchez-Azofeifa G.A., Quesada M., Rodríguez J.P., Nassar M., Stoner K.E., Castillo A., Garvin T., Zent E.L., Calvo J.C., Kalacska M., Fajardo L., Gamon J., Cuevas-Reyes P. 2005. Research Priorities for Neotropical Dry Forests. Biotropica, in press.

Schlerf M., Atzberger C., Hill J., 2005. Remote sensing of forest biophysical variables using HyMap imaging spectrometer data. Remote sensing of environment in press.

Schowengerdt R.A., 1996. On the estimation of spatial-spectral mixing with classifier likelihood functions. Pattern recognition letters 17, 1379-1387.

Sims D.A., Gamon J.A., 2002. Relationships between leaf pigment content and spectral reflectance across a wide range of species, leaf structure and developmental stages. Remote sensing of Environment 81, 337-354.

Sims D.A., Gamon J.A., 2003. Estimation of vegetation water content and photosynthetic tissue area from spectral reflectance: a comparison of indices based on liquid water and chlorophyll absorption features. Remote Sensing of Environment 84, 526-537.

Steininger M.K. 1996. Tropical secondary forest regrowth in the Amazon: age, area and change estimation with Thematic data. International Journal of Remote Sensing 20:839-877.

Steininger M.K. 2000. Satellite estimation of tropical secondary forest above-ground biomass: data from Brazil and Bolivia. International Journal of Remote Sensing 21:1139-1157.

Stern M., Quesada M., Stoner K.E. 2002. Changes in composition and structure of a tropical dry forest following intermittent cattle grazing. Revista de Biologia Tropical 50:1021-1034.

Thenkabail P.S., Nolte C., Lyon J.G., 2004. Remote sensing and GIS modeling for selection of a benchmark research area in the inland valley agroecosystems of West and Central Africa. Photogrammetric engineering and remote sensing 66, 755-768.

Townshend J., Justice C., Li W., Gurney C., Mcmanus J., 1991. Global land cover classification by remote sensing - present capabilities and future possibilities. Remote sensing of environment 35, 243-255.

Tuner D.P., Cohen W.B., Kennedy R.E., Fassnacht K.S., Briggs J.M., 1999. Relationships between leaf area index and Landsat TM spectral vegetation indices across three temperate zone sites. Remote sensing of environment 70, 52-68.

Tuomisto H., Poulsen A.D., Ruokolainen K., Moran R.C., Quintana C., Celi J., Canas G. 2003. Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. Ecological Applications. 13:352-371.

Turner W., Sepctor S., Gardiner N., Fladeland M., Sterling E., Steininger M. 2003. Remote sensing for biodiversity science and conservation. *Trends in Ecology and Evolution* 18: 306-314

Webb L.J., Tracey J.G., Williams W.T. 1972. Regeneration and pattern in the subtropical rain forest. Journal of Ecology 60:675-695.

Zhang J., Rivard B., Sanchez-Azofeifa G.A. Intra and inter-class spectral variability of tropical tree species at La Selva, Costa Rica: Implications for species identification using HYDICE imagery. *Remote Sensing of Environment*. Submitted 2005.

Table 6.1 Summary of the biophysical and diversity characteristics per successional stage.

Stage	Height	Basal area	Stem density	Species density	Shannon diversity	Biomass	HCI
Early	7.5±2.2 (4.6-11.5)	11.7±5.4 (3-19)	112±64 (21-195)	15±7 (5-28)	1.77±0.56 (0.57-2.65)	5.6±3.3 (1.1-10.9)	28.0±36.0 (0.5-121.1)
Intermediate	10.3±3.4 (6.7-15.8)	21.4±6.8 (13-32)	130±35 (51-177)	29±5 (23-5)	2.88±0.36 (2.14-3.36)	10.9±4.6 (5.8-17.0)	68.8±57.7 (27.4-129.8)
Late	15.0±2.2 (12.7-17.5)	30.1±6.5 (21-39)	107±42 (88-209)	29±7 (22-40)	2.75±0.56 (2.22-3.39)	16.0±4.3 (10.5-23.4)	159.0±57.7 (110.2-235.8)

Data indicates mean ± standard deviation with the values in parentheses representing the range. Height is measured in meters, basal area in m2/ha, stem density in No. stems/0.1ha, species density in No. species/0.1ha, biomass in t/0.1ha and Shannon diversity and HCI are unit less. Data adapted from Kalacska et al. (2004) and Kalacska et al. (2005b).

Table 6.2 Spectral vegetation indices used in this study

Spectral Vegetation Index	Formula
NDVI	$(R_{800}-R_{680})/(R_{800}+R_{680})$
mNDVI	$(R_{750}-R_{705})/(R_{750}+R_{705})$
SR	R_{800}/R_{680}
mSR	R_{750}/R_{705}
MSR	$\frac{\frac{R_{800}}{R_{680}-1}}{\sqrt{\frac{R_{800}}{R_{680}}+1}}$
CSI	$2sSR-sSR^2+SWI^2$ where: $sSR = \frac{\frac{R_{800}}{R_{680}}-1}{(\frac{R_{800}}{R_{680}}-1)_{max}}$ $SWI = \frac{\frac{R_{900}}{R_{1180}}-1}{(\frac{R_{900}}{R_{1180}}-1)_{max}}$

Table 6.3 Results from the best fit validation models for estimating the forest characteristics. The best model for each characteristic was the Wavelet decomposition followed by a stepwise regression.

Forest characteristic	Image	R^2
Biomass	March	0.82
Height	March	0.90
Basal area	March	0.71
Shannon species richness	March	0.83
Holdridge Complexity Index	March	0.60
Species density	March	0.34
Stem density	March	0.20

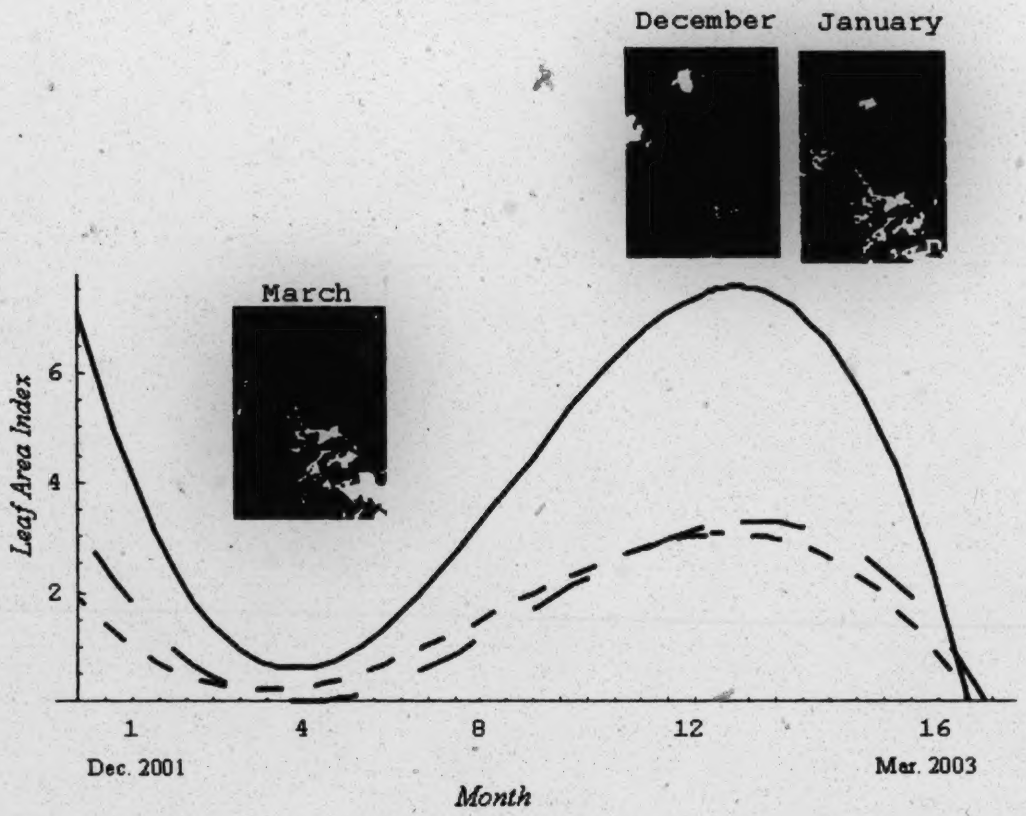

Figure 6.1 Hyperion images for Santa Rosa National Park (March, December and January) superimposed above the leaf phenological cycles for the early (dashed), intermediate (long dashes) and late (solid) stages. Reprinted from Tree Physiology, 25, Kalacska, Calvo-Alvarado, Sanchez-Azofeifa G.A. Calibration and assessment of seasonal changes in leaf area index of a tropical dry forest in different stages of succession, 733-744 Copyright (2004), with permission from Heron Publishing.

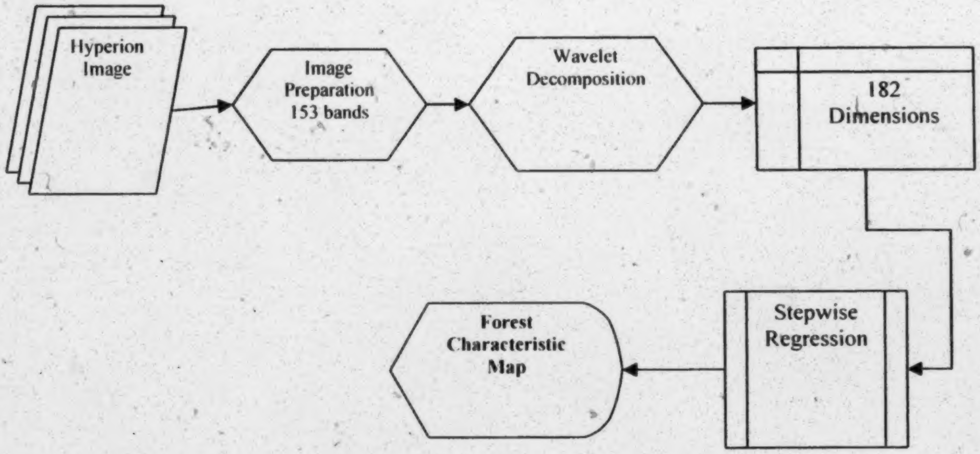
Hyperion Image
Image Preparation 153 bands
Wavelet Decomposition
182 Dimensions
Stepwise Regression
Forest Characteristic Map

Figure 6.2 Final image processing methodology for estimating forest structure, biomass and species richness from the March Hyperion image.

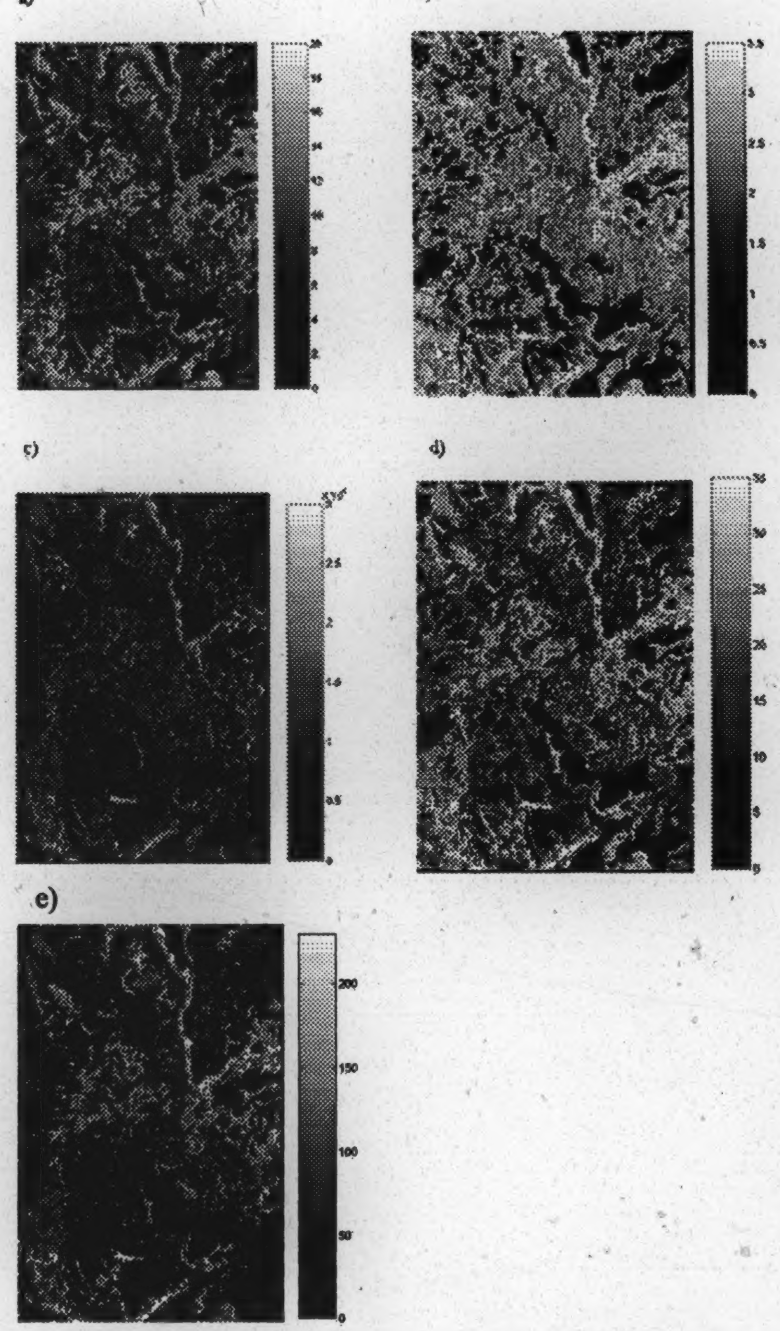
a)
20
18
16
14
12
10
8
6
4
2
0
b)
3.5
3
2.5
2
1.5
1
0.5
0
c)
x10^5
2.5
2
1.5
1
0.5
0
d)
35
30
25
20
15
10
5
0
e)
200
150
100
50
0

Figure 6.3 Resulting forest structure, biomass and species richness maps estimated from the March Hyperion image. a) canopy height (m), b) Shannon species richness, c) biomass (kg) d) basal area (m2/ha) e) Holdridge complexity index

Chapter 7: Conclusions and Future Work

7-1. Synthesis of significant contributions

One of the earliest studies one finds listed in the Science Citation Abstracts when searching for tropical dry forests is Gentry (1969), which is a comparison of leaf characteristic between dry and wet forest species. However, naturalist accounts do go much farther back. For example, T. Belt (1874) published the first description of *Acacia collinsii* and its symbiotic relationship with *Pseudomyrmex* sp. ants; a classic example of plant-animal interactions currently present in the tropical dry forest. Subsequent landmark publications regarding tropical dry forests include *Life Zone Ecology* (Holdrige 1967), and *Costa Rican Natural History* edited by D. Janzen (1983). While not focusing exclusively on Neotropical dry forests, these publications highlight the unique physical (i.e. climate), biological and ecological characteristics of the tropical dry forest. Nevertheless, the intrigue of the Neotropical dry forest was soon lost to the romanticism of the rain forests and it wasn't until the 1990's that Neotropical dry forest research began to very slowly regain popularity (Sanchez-Azofeifa et al. 2005). A significant publication from the 1990's was a multi-site, multi-disciplinary volume *Seasonally Tropical Forests* edited by Bullock et al. (1995).

Overall, the majority of the studies in Neotropical dry forests have focused on certain specific elements: descriptions of flower phenology, pollination and floral reproductive traits (Janzen 1967, 1971, Haber and Frankie 1982, Frankie et al. 1997, James et al. 1998, Lobo et al. 2003); descriptions of species assemblages (Chapman 1988, Flemming 1988, Rodriguez and Chinchilla 1996, Segura et al.

2003, Quigley and Platt 2003); watershed management (Pringle and Scatena 1999, Pringle 2000); similarities and differences between dry and wet forests (Gentry 1995); effects of water stress (Medina 1995); biomass (Murphy and Lugo 1986); effects of fragmentation (Stoner et al. 2003); and recovery following natural disturbances such as hurricanes (Ayala-Silva and Twumasi 2004). In more recent years there has also been a shift into examining this ecosystem from a remote sensing perspective (Sanchez-Azofeifa et al. 2003, Arroyo-Mora et al. 2005a,b, Fajardo et al. 2005) and correlating findings with physiological processes or differences (Castro et al. 2004, Sanchez-Azofeifa and Castro 2005, Gamon et al. 2005). Nonetheless as described in Sanchez-Azofeifa et al. (2005), the attention focused on the tropical dry forest is extremely limited in comparison to what is known about their wet counterparts.

In the preceding chapters I have presented a compilation of studies evaluating the structure and diversity of the Neotropical dry forest by means of remotely sensed data moving from a large scale (ecosystem level) to a micro-level (leaf level). Throughout all the chapters the recurring theme is the importance of the spectro-temporal domain in an ecosystem as dynamic as the dry forest. In the following section I discuss the main findings and their relevance in the scope of future tropical dry forest research.

The results from Chapter 2: "*Quantifying tropical forest extent and payments for environmental services from satellite imagery*" demonstrate that one of the fundamental issues that still precludes sound comparative analysis of land cover datasets is semantics. This lack of standardization is linked to the use and incorporation of data that are tailored to the needs of various disciplines such as remote sensing, forestry, and ecology; thus preventing direct commensurability between attributes and descriptions. Recently, the Tropi-Dry network (Sanchez-Azofeifa et al. 2005) proposed a new concise definition for the tropical dry forest which would be applicable and transferable to both ecology and remote sensing as a means to circumvent this problem. However, the international acceptance of use the definition in practice remains to be seen. It was also highlighted in Chapter 2 that the discrepancies caused by something as simple as "how much forest is there?" is propagated to any subsequent use of the data. The magnitude of these discrepancies is clearly seen when they are translated from km^2 of forest to net worth of environmental services ($), and estimates of total ecosystem carbon. Errors and uncertainties of 20-32M$ in the estimation of environmental services (at the country scale for a country the size of Costa Rica) as shown in Chapter 2 would not promote trust in the Annex B countries and other investors. The preexisting ecosystem biased towards the tropical evergreen forests referred to by Redford et al. (1990) is also shown by the obvious overestimation of the evergreen (wet) forest by every land cover classification examined (Chapter 2). This evergreen forest bias is also echoed by the lack of past research in the tropical dry forest as presented in Chapter 1 in comparison to the tropical wet (evergreen) forest.

At another scale Chapter 3; "*Calibration and assessment of seasonal changes in leaf area index of a tropical dry forest in different stages of succession*" highlights the asynchronous phenological cycles of the different successional stages, a factor that links directly to the concept of the spectro-temporal domain. This finding is important for projects making use of remote sensing technology in the dry forest in planning optimal times for image acquisition and interpretation especially since during certain months of the year the intermediate successional stage is indistinguishable from the others. This importance of the "spectro-temporal" domain is also addressed in Chapter 6: "*Ecological fingerprinting of ecosystem succession: estimating secondary tropical dry forest structure and diversity using imaging spectroscopy*". By illustrating the changes in the spectral signature of the successional stages it was shown that the optimal time for extracting forest structure and diversity from imagery is in March (dry season) which corresponds to minimal foliage and a point in the phenological cycle where all three stages are distinct (Chapter 3). Chapter 3 also addresses the complication to remotely sensed studies imposed by lianas with the finding that lianas retain their leaves until well after their host trees. Issues of calibration and data integration are also addressed in Chapter 3. The methodology described for collecting and calibrating optical leaf area index data (LAI) is a means to ensure that canopy characteristic measured on the ground will be comparable and relatable to imagery. It circumvents the collection of data that is unsuitable for the type of analyses that may be planned (e.g. use of inappropriate sampling scheme for relating to imagery or other data).

The study in Chapter 4: "*Estimating leaf area index from satellite imagery using Bayesian Networks*" is the first to use Bayesian Networks to estimate an ecological variable such as LAI from satellite imagery. To date such studies were conducted with classical statistics (i.e. regression models) or neural networks (Hall et al. 1995, Atzberger 2004, Kalacska et al. 2004). The results of this study demonstrate not only the predictive power of Bayesian Networks but also their explanatory power, in general, far beyond what is typically available with current pixel classifiers (Jensen 2001). The other innovation presented in the results is a map of the confidence in the predictions of LAI. This allows for assessing regions within the study area that may be problematic or need additional clarification such as the early successional stage (sparse canopy) whose spectral signature in the wet season resembles more developed stages because of the thick understory of grasses and shrubs.

A combination of both climate and past land use/management practices were found to be the major contributing factors to structural differences among three Mesoamerican dry forest sites (Chapter 5: "*Effects of seasonal and successional stage on leaf area index and spectral vegetation indices in three Mesoamerican tropical dry forests*"). The vertical component of the canopy structure (i.e. number of layers) varied the most between sites rather than the horizontal component (i.e. canopy openness). For all sites in the wet season, the height of the canopy was the most influential factor affecting plant area index. For the dry season only canopy openness (from the dry season) was significant, highlighting the importance of the contribution of the non-photosynthetic component of the canopy. The importance of the woody component of the canopy is also highlighted in Chapter 3 where it is shown that in the dry season optical estimations overestimate LAI by the contribution of the woody components.

7-2. Challenges to come

One consideration for future tropical dry forest research is the continual incorporation of data analysis techniques from other communities such as machine learning and pattern recognition (*IEEE transactions on pattern analysis and machine intelligence*), signal processing *(IEEE transactions on signal processing)*, geostatistics (Stein et al. 1999), wavelet analysis (Misiti et al. 1996), Bayesian networks (Jensen 1991), neural networks *(IEEE transactions on neural networks)*, etc. These communities have developed several techniques that would allow more elegant and robust analyses rather than relying solely on traditional methods of data analysis. Ecology and remote sensing are becoming increasingly experimental sciences where data is collected to test hypotheses and answer pertinent research questions (Scheiner and Gurevitch 2001). However, the nature of the data collected poses certain problems such as the violation of basic statistical assumptions, limited repetition or contrarily very large data sets. Therefore, techniques that may not yet be common in ecology or remote sensing but may be more suited to the data and the questions being addressed are worth investigating.

One of the predominant challenges in the near future is the need to expand on the concept of classifying, describing and analyzing the tropical dry forest (and possible the wet forest as well) by successional stage rather than "age." In the wet forest age has been used extensively to describe plots of secondary forest (Lucas et al. 2000, Chazdon et al. 2005); those assignments have been further used to partition the data for analysis and discussion. I believe this is a fundamentally wrong approach for the dry forest. It has been shown that because of its complex land use history, the dry forest does not respond or regenerate homogeneously in structure or composition following abandonment (Kalacska et al. 2004, Arroyo-Mora et al. 2005). Nevertheless the habit of partitioning the forest by age is a convention that is proving to be very difficult to change. The only instance I believe that "age" can be used as an accurate descriptor of an area under regeneration is under a controlled scenario such as the BDFFP (Biological Dynamics of Forest Fragments Project) project conducted north of Manaus, Brazil in the Amazon. In that scenario primary forest with no recent history of having been subjected to anthropogenic disturbance was cleared at specific intervals and is being monitored and compared to primary forest as it regenerates. This however, is a very isolated example of using "age" to categorize forest regeneration. A comprehensive analysis of the data collected at the current Tropi-Dry network research sites in Costa Rica, Mexico, Venezuela, Cuba and Brazil (both ecological and remotely sensed) comparing site characteristics partitioned by age and successional stage would be a first step towards convincing the tropical ecology/biology and remote sensing communities to shift their focus from "*age*" to "*stage*".

The second area of future research I would like to highlight is the spatial assessment of the dynamics of dry forest regeneration. This topic considers the application of analysis techniques such as those presented in Chapter 6 for the mapping of forest structure and diversity over time and the subsequent spatial analysis of the patterns and trends that are seen. Such initiative would entail a long term monitoring plan of the forest (i.e. 5-10 years) through a series of structure and diversity maps created from hyperspectral imagery. Specific successional stages and their regeneration could be tracked in terms of their structural traits which when combined with diversity may be more informative than diversity alone. Ephemeral, dynamic and lasting areas (pockets) of high and low species richness could be highlighted by this type of analysis. Such could further lend supporting evidence (or not) or find similarities to theories of succession and diversity such as those presented in Budowski (1965), Webb et al. (1972), Connell (1978), Hubbell (1979, 2001) among others. Furthermore, following the initiative presented above, the application of airborne hyperspectral imagery from sensors such as HyMap need to be explored to improve the predictions of ecosystem structure and diversity. The HyMap instrument (Cocks et al. 1998) collects hyperspectral images with 128 bands from 400-2500nm with a spectral bandwidth of 15-20nm. With a 60° field of view, the spatial resolution of the imagery would 10m if flown at an altitude of 4km (Figure 7.1). Radiometric calibration of HyMap data has been shown to have errors of 2-3% (or less) (Richter et al. 2002). The application of this type of imagery will allow for more detailed finer scale analyses of the dynamics of the tropical dry forest. As described in Chapter 3, in the intermediate successional stage, lianas comprise a substantial part of the forest biomass. Being able to quantify their actual spatial extent over the canopy and subsequently monitor any significant changes would be an important step towards understanding their contribution to canopy reflectance, response to climate change and effects on forest biodiversity.

7-3. References

Arroyo-Mora J.P., Sanchez-Azofeifa G.A., Kalacska M.E.R., Rivard B., Calvo-Alvarado J.C., Janzen D.H.(2005) Secondary forest detection in a Neotropical dry forest landscape using Landsat 7 ETM+ and IKONOS imagery. *Biotropica* **37** in press.

Arroyo-Mora J.P., Sanchez-Azofeifa G.A., Rivard B., Calvo J.C., Janzen D.H.(2005) Dynamics in landscape structure and composition for the Chorotega region, Costa Rica from 1960 to 2000. *Agriculture, Ecosystems and Environment* **106** 27-39.

Atzberger C.(2004) Object-based retrieval of biophysical canopy variables using artificial neural nets and radiative transfer models. *Remote Sensing of Environment* **93** 53-67.

Ayala-Silva T, Twumasi YA(2004) Hurricane Georges and vegetation change in Puerto Rico using AVHRR satellite data. *International Journal of Remote Sensing* **25** 1629-1640.

Belt T. (1874) The Naturalist in Nicaragua. John Murray, London.

Budowski G.(1965) Distribution of tropical American rain forest species in the light of successional processes. *Turrialba* **15** 40-42.

Bullock S.H., Mooney H.A., Medina E. (1995) Seasonally dry tropical forests. University of Cambridge Press, Cambridge.

Castro-Esau KL, Sanchez-Azofeifa GA, Caelli T(2004) Discrimination of lianas and trees with leaf-level hyperspectral data. *Remote sensing of environment* **90** 353-372.

Chapman C.A.(1988) Patterns of foraging and range use by three species of Neotropical primates. *Primates* **29** 177-194.

Chazdon RL, Brenes AR, Alvarado BV(2005) Effects of climate and stand age on annual tree dynamics in tropical second-growth rain forests. *Ecology* **86** 1808-1815.

Clark ML, Roberts DA, Clark DB(2005) Hyperspectral discrimination of tropical rain forest tree species at leaf to crown scales. *Remote Sensing of Environment* **96** 375-398.

Cocks T., Jenssen R., Stewart A., Wilson I., and Shields T. The HyMap airborne hyperspectral sensor: the system, calibration and performance. First EARSeL Workshop on Imaging Spectroscopy. 98. Paris, EARSeL.

Connell J.H.(1978) Diversity in tropical rain forests and coral reefs. *Science* **199** 1302-1310.

Fajardo L., Gonzales V., Nassar J. , Lacabana P., Portillo C.A., Carrasquel F., Rodriguez J.P.(2005) Tropical dry forests of Venezuela: Characterization and current conservation status. *Biotropica* **37** in press.

Flemming T. H. (1988) The short-tailed fruit bat: A study in plant-animal interactions . University of Chicago Press, Chicago.

Frankie G.W., Baker H.G., Opler P.A.(1974) Comparative phenological studies of trees in tropical wet and dry in the lowlands of Costa Rica. *Journal of Ecology* **62** 881-919.

Gamon J.A., Kitajima K., Mulkey S.S., Serrano L., Wright S.J.(2005) Diverse optical and photosynthetic properties in a Neotropical dry forest during the dry season: Implications for remote estimation of photosynthesis. *Biotropica* **37** in press.

Gentry A.H.(1969) A comparison of some leaf characteristics of tropical dry forest and tropical wet forest in Costa Rica. *Turrialba* **19** 419-.

Gentry A.H. (1995) Diversity and floristic composition of neotropical dry forests. In:Seasonally Tropical Forests (eds Bullock S.H., Mooney H.A., Medina E.), pp. 147-194. Cambridge University Press, Cambridge.

Haber W.A., Frankie G.W.(1982) Pollination ecology of *Luhea* (Tiliacea) in Costa Rican deciduous forest. *Ecology* **63** 1740-1750.

Hall F.G., Townshend J.R., Engman E.T.(1995) Status of remote sensing algorithms for the estimation of land surface state parameters. *Remote Sensing of Environment* **85** 257-270.

Holdridge L. (1967) Life zone ecology. Tropical Science Center, San Jose, Costa Rica.

Hubbell S.P.(1979) Tree dispersion, abundance, and diversity in a tropical dry forest . *Science* **203** 1299-1309.

Hubbell S.P. (2001) The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton.

James T., Vege S., Aldrich P., Hamrick J.L.(1998) Mating systems of three tropical dry forest species. *Biotropica* **30** 587-594.

Janzen D.H. (1983) Costa Rican Natural History. University of Chicago Press, Chicago.

Janzen D.H.(1971) Euglossine bees as long-distance pollinators of tropical plants. *Science* **171** 203-205.

Janzen D.H.(1967) Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution* **56** 841-854.

Jensen F.V. (2001) Bayesian Networks and Decision Graphs. Springer-Verlag, New York.

Kalacska M., Sanchez-Azofeifa G.A., Rivard B., Calvo-Alvarado J.C., Journet A.R.P. , Arroyo-Mora J.P., Ortiz-Ortiz D.(2004) Leaf area index measurements in a tropical moist forest: A case study from Costa Rica. *Remote Sensing of Environment* **91** 134-152.

Kalacska M, Sanchez-Azofeifa GA, Calvo-Alvarado JC, Quesada M, Rivard B, Janzen DH(2004) Species composition, similarity and diversity in three successional stages of a seasonally dry tropical forest. *Forest Ecology and Management* **200** 227-247.

Lobo J.A., Quesada M., Stoner K.E., Fuchs E.J., Herrerias-Diego Y., Rojas-Sandoval J., Saborio-Rodriguez G.(2003) Factors affecting phenological patterns of Bombacaceous trees in seasonal forests in Costa Rica and Mexico. *American Journal of Botany* **90** 1054-1063.

Lucas RM, Honzak M, Curran PJ, Foody GM, Milne R, Brown T, Amaral S(2000) Mapping the regional extent of tropical forest regeneration stages in the Brazilian Legal Amazon using NOAA AVHRR data. *International Journal of Remote Sensing* **21** 2855-2881.

Medina E. (1995) Diversity of life forms of higher plants in Neotropical dry forests. In:Seasonally dry tropical forests (eds Bullock S.H., Mooney H.A., Medina E.), pp. 221-242. Cambirdge University Press, Cambridge.

Misiti M., Misiti Y. , Oppenheim G., Poggi J.M. (1996) Wavelet Toolbox User's Guide . The Mathworks Inc., Natick MA..

Murphy P.G., Lugo A.E.(1986) Structure and biomass of a subtropical dry forest in Puerto Rico. *Biotropica* **18** 89-96.

Pringle C.M., Scatena F. (1999) Aquatic ecosystem deterioration in Latin America and the Caribbean. In:Managed ecosystems: The Mesoamerican experience (eds Hupton Hatch L., Swisher M.E.), pp. 104-113. Oxford University Press, New York.

Quigley M.F., Platt W.J.(2003) Composition and structure of seasonally deciduous forests in the Americas. *Ecological Monographs* **7** 87-106.

Redford K.H., Taber A, Simonetti J.A.(1990) There is more to biodiversity than the tropical rain-forests. *Conservation Biology* **4** 328-330.

Richter R., Muller A., Heiden U.(2002) Aspects of operational atmospheric correction of hyperspectral imagery. *International Journal of Remote Sensing* **23** 145-157.

Rodriguez F.J., Chinchilla F.A.(1996) List de mammiferos de Costa Rica. *Revista de Biologia Tropical* **44** 877-890.

Sanchez-Azofeifa G.A., Castro-Esau K.L.(2005) Canopy observations on the hyperspectral properties on a community of tropical dry forest lianas and their host trees. *International Journal of Remote Sensing* **in press** .

Sanchez-Azofeifa G.A., Quesada M., Rodriguez J.P., Nasser J.M., Stoner K.E., Castillo A., Garvin T., Zent E.L., Calvo J., Kalacska M., Fajardo L., Gamon J., Cuevas-Reyes P.(2005) Research priorities for Neotropical dry forests. *Biotropica* **in press** ..

Scheiner S.M, Gurevich J. (2001) Design and Analysis of Ecological Experiments. Oxford University Press, Oxford.

Segura G., Balvanera P., Duran E., Perez A.(2003) Tree community structure and stme mortality along a water availability gradient in a Mexican tropical dry forest. *Plant Ecology* **169** 259-271.

Stein A., Van der Meer F., Gorte B. (1999) Spatial statistics for remote sensing. Kluwer Academic Publishers, London.

Stoner K.E., Quesada M., Rosas-Guerrero, Lobo J.A.(2003) Effects of forest fragmentation on Colima long-noed bat foraging in tropical dry forest in Jalisco, Mexico. *Biotropica* **34** 462-467.

Webb L.J, Tracey J.G., Williams W.T.(1972) Regeneration and pattern in the subtropical rain forest. *Journal of Ecology* **60** 675-695.

Figure 7.1 Example of a HyMap image (3-5m spatial resolution) collected March 30, 2005 over Los Inocentes, Guanacaste, Costa Rica.

Appendix 3.3. Specific leaf area for 63 plant species from Santa Rosa National Park. Abbreviations: SLA=specific leaf area; and CV=coefficient of variation.

Species	**Family**	**SLA (cm^2/g)**	**CV (%)**
Acosmium panamensis	Fabaceae Papilionodeae	179.4	31.5
Agonandra macrocarpa	Opiliaceae	166.0	25.1
Albizia adinocephala	Fabaceae Mimosoideae	180.2	6.9
Alibertia edulis	Rubiaceae	102.1	4.2
Allophylus occidentalis	Sapindaceae	304.0	2.1
Annona pourpourea	Annonaceae	315.6	16.7
Annona reticulate	Annonaceae	320.7	13.7
Apeiba tibourbou	Tiliaceae	171.2	6.8
Aphelandra scabra	Acanthaceae	278.6	7.7
Ardisia revolute	Myrsinaceae	108.1	14.5
Arrabidaea mollissima	Bignonaceae	163.0	7.5
Ateleia donnell-smithii	Fabaceae Papilionodeae	188.5	2.0
Bauhinia ungulate	Fabaceae Caesalpinaceae	245.8	14.8
Banisteriopsis cornifolia	Malpighiaceae	240.8	8.4
Banisteriopsis muricata	Malpighiaceae	210.5	20.7
Bursera simarouba	Burseraceae	222.7	9.6
Bursera tomentosa	Burseraceae	322.4	5.4
Byrsonima crassifolia	Malpighiaceae	143.6	4.2
Calycophyllum candidisimum	Rubiaceae	224.0	5.1
Capparis indica	Capparidaceae	77.6	4.2
Casearia silvestris	Flacourtaceae	190.8	7.0
Cedrela odorata	Meliaceae	289.6	3.3
Chromolaena glaberrima	Asteraceae	285.8	5.9
Cochlospermum vitifolium	Cochlospermaceae	116.0	11.7
Convolvulus nodiflorus	Convolvulaceae	496.2	20.2
Cordia alliodora	Boraginaceae	190.3	47.6
Curatella americana	Dillenaceae	78.7	11.7
Cydista diversifolia	Bignonaceae	184.9	25.2
Erythroxylum havanense	Erythroxylaceae	208.7	15.0
Euphorbia schlenchtendalii	Euphorbiaceae	370.3	5.6
Exostema mexicanum	Rubiaceae	476.5	15.4
Forsteronia spicata	Apocynaceae	243.5	6.5
Genipa americana	Rubiaceae	140.6	38.4
Gliricida sepium	Fabaceae Papilionodeae	215.6	11.1
Guazuma ulmifolia	Sterculiaceae	108.0	11.5
Guettarda macrocarpa	Rubiaceae	200.1	2.8
Helicteres baruense	Sterculiaceae	196.9	3.4

Lippia verlandreri	Verbenaceae	231.7	26.7
Lonchocarpus felipei	Fabaceae Papilionodeae	190.8	6.0
Luhea speciosa	Tiliaceae	157.4	16.0
Lygodium venustrum	Schizaeaceae	435.2	39.1
Machaerium bivolatum	Fabaceae Papilionodeae	273.5	5.2
Maclura tinctoria	Moraceae	456.8	10.1
Mucuna urens	Fabaceae Papilionodeae	414.0	6.3
Psychotria horizontalis	Rubiaceae	181.3	8.8
Quercus oleoides	Fagaceae	80.2	6.5
Randia monantha	Rubiaceae	291.9	9.7
Randia thurberi	Rubiaceae	266.8	21.5
Rehdera trinervis	Verbenaceae	103.2	2.3
Roupala montana	Proteaceae	70.5	9.3
Sciadodendron excelsum	Araliaceae	634.7	5.5
Sebastiana confusa	Euphorbiaceae	309.5	12.0
Sebastiana pavoniana	Euphorbiaceae	261.8	6.4
Semiliarium mexicanum	Hippocrataceae	140.8	11.2
Simarouba glauca	Simaroubaceae	113.9	3.9
Spondia purpurea	Anacardiaceae	498.9	8.5
Stemmadenia obovata	Apocynaceae	308.7	11.6
Swietenia macrophylla	Meliaceae	119.2	12.3
Tabebuia ochracea	Bignonaceae	262.1	6.3
Tetracera volubilis	Dillenaceae	215.6	4.3
Trichilia martiana	Meliaceae	199.2	9.9
Trichilia trifolia	Meliaceae	401.1	32.3
Xylophragma seemannianum	Bignonaceae	213.3	16.1